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Bureau of Commercial Fisheries

FISHERY BULLETIN

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UNITED STATES DEPARTMENT OF THE INTERIOR
U.S. FISH AND WILDLIFE SERVICE
BUREAU OF COMMERCIAL FISHERIES

FISHERY BULLETIN

VOLUME 66, No. 2

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Created in 1849, the U.S. Department of the Interior is concerned with the management, conservation, and development of the Nation's water, fish, wildlife, mineral, forest, and park and recreational resources. It also has major responsibilities for Indian and Territorial affairs.

As the Nation's principal conservation agency, the Department works to assure that nonrenewable resources are developed and used wisely, that park and recreational resources are conserved for the future, and that renewable resources make their full contribution to the progress, prosperity, and security of the United States—now and in the future.

OBJECTIVE STUDIES OF SCALES OF COLUMBIA RIVER CHINOOK SALMON, *ONCORHYNCHUS TSHAWYTSCHA* (WALBAUM)[1]

BY

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ABSTRACT

This study uses an objective method that measures and graphs the spacings of circuli. It also introduces a new method of differentiating ocean nucleus from stream nucleus. Four groups of chinook salmon scales were studied, each with a specific purpose.

First, scales from recoveries of two kinds of marked fall chinook at Spring Creek National Fish Hatchery were compared: one kind was from fish released as fry, and the other from fish released as fingerlings. In the nuclear part of scale growth, the group released as fry showed a larger variance in spacing of circuli than the group released as fingerlings but the difference in the mean values between these two groups was not significant. In the first marine part of scale growth, circulus spacing was significantly wider in the group released as fry than in the group released as fingerlings. It was not possible, however, to identify individual scales as coming from fish released as fry or as fingerlings.

Second, scales from marked and unmarked fall chinook salmon at Spring Creek Hatchery were compared to see if any effect of marking could be detected. Significant differences in circulus spacing in marine growth existed between marked and unmarked fish, the latter having wider spacings. Marking was in the removal of adipose and right pectoral fins from chinook fingerlings. This technique was therefore regarded as having unfavorably affected the growth of marked fish.

Third, scales from marked fall chinook that had been released at various times of the year at Little White Salmon National Fish Hatchery were studied. The scales showed that young chinook salmon released in May and July of the first year grew an ocean nucleus typical of fall chinook; those released in February of the second year grew a stream nucleus typical of spring chinook; and those released in September and October of the first year grew a nucleus intermediate in character.

Fourth, scales of fall and spring chinook salmon were studied to see how these two groups could be identified by their scales. Measurements of circulus spacing in the first and second summer of marine growth revealed that, in the spring chinook, marine circuli in both summers were about equally wide; whereas, in the fall chinook, marine circuli of the second summer were nearly one and one-half times wider than those of the first summer. Thus, these scales can be distinguished, not by nuclear growth as is normally done by subjective judgment, but by relative marine growth as measured by objective means.

Since the early studies on the scales of chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), by Gilbert (1914), Rich (1922), Rich and Holmes (1929), and others, little has been published on the subject. Many problems still deserve further study. The most important and interesting problem is the classification and identification of nuclear growth zones, the central part of scale growth. Gilbert (1914) classifies chinook scales into two types: those with an ocean nucleus and those with a stream nucleus. The ocean nucleus type originates from fish that migrate seaward in their first year and thus has the first annulus at the end of the first year's marine growth; the stream nucleus type originates from fish that do not migrate seaward until the early months of the second year and thus has the first annulus at the end of fresh-water growth. To the former group belongs the fall run of chinook, which enters the river from July through November; to the latter, the spring run, which enters the river from March to June.

Classification of nuclear growth zones is very useful and today still serves as the foundation of age study of chinook salmon. This method is most useful when only two groups of chinook salmon are involved and their nuclear zones

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Published April 1967.

are clearly defined. Its application becomes limited, however, when the boundaries of nuclear growth are not clear-cut. The chinook salmon young of the Columbia River, for instance, migrate seaward throughout most of the year (Rich, 1922); consequently, the first year's growth is subject to numerous variations that intergrade so completely that it is impossible to draw any sharp line of distinction (Rich and Holmes, 1929). Most Columbia River chinooks, according to Rich and Holmes (1929), have neither typical stream nor typical ocean nuclei, but apparently have spent part of the first year in fresh water and part in the ocean. The result has been a nuclear area composed in part of stream growth with narrowly spaced circuli and in part of ocean growth with widely spaced circuli to form what these authors term "composite nucleus."

The composite nucleus makes age determination difficult. In a composite nucleus, the amount of stream growth varies inversely with the amount of ocean growth. At one extreme is the type with only a small amount of stream growth accompanied by a large amount of ocean growth. At the other extreme is the type with a great amount of stream growth accompanied by a small amount of ocean growth. The first type of nuclear growth approaches the ocean nucleus, and the second type approaches the stream nucleus. Between these two extremes there are complete intergradations. This poses the question: "Where should the annuli be placed, and how many?"

The question is further complicated by the formation of the so-called "intermediate growth," that is, growth of circuli in the estuary while the fish is migrating seaward. Circuli of this growth cannot be distinguished with certainty from either the stream or the ocean circuli, and they often form a check which, in the words of Rich and Holmes, "might easily be mistaken for an annulus by an inexperienced observer." These same authors maintain that with experience this kind of error may be eliminated almost completely, and that their own experience with the scales of fish of known history has provided sufficient information for correct age determination.

The prerequisite of experience in scale reading cannot be denied, but the dependence upon experience can be lessened and the accuracy of age determination improved if some mechanical method in scale work can be developed so that the scale growth and marks can be interpreted more objectively. The development of an objective method is the major purpose of the present work. From a large number of scales collected from chinook salmon of known ages through recoveries of marked fish, we were able to establish some definite criteria and methods whereby one can objectively interpret scale marks with a minimum amount of guess work.

The present study comprises four parts. First, scales from adult fall chinook that have migrated seaward as unfed fry and as fed fingerlings[4] were compared in an attempt to find characteristics that might serve to identify fish of unknown origin; i.e., whether they come from fry migrants or from fingerling migrants.

Second, comparative studies were made between scales from fall chinook that had been fin-clipped when released as fingerlings and those that had not been marked. This was to see if marking had any adverse effect on growth that could be detected by scale measurements.

Third, marking experiments on young fall chinook performed by U.S. Fish and Wildlife Service personnel at the Little White Salmon Hatchery provided an unusually valuable series of adult scale samples for age and growth study. Young chinook salmon were released over a wide range of time (May to February), and each release had a different mark. Scales from returned adults originating from different releases were studied to gain insight into the formation of a fresh-water annulus and to assess the relative amount of first and second year's ocean growth due to different release dates. This provided valuable information for understanding scale growth patterns in fall and spring chinooks.

Fourth, the relative amount of the first and second year's ocean growth on scales in known stocks of fall and spring chinooks was studied and compared. An objective method of determining the presence or absence of an annulus in nuclear growth and therefore in distinguishing fall and spring chinooks was developed, independent of fresh-water growth itself.

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[4] "Fed fingerlings" refers to young chinook salmon that have been fed for about 3 months.

MATERIALS AND METHODS

Materials for the present study were supplied by the Fish Commission of Oregon and by the Portland Program Office of the Bureau of Commercial Fisheries of the U.S. Fish and Wildlife Service. Scale impressions on cellulose acetate cards of the following were available for study.

1. Returns of marked fall chinook to Spring Creek Hatchery:
    a. 1958 returns—released as fry, 1 fish; released as fingerlings, 8 fish.
    b. 1959 returns—released as fry, 8 fish; released as fingerlings, 173 fish.
    c. 1960 returns—released as fry, 28 fish; released as fingerlings, 158 fish.
2. Returns of unmarked fall chinook to Spring Creek Hatchery:
    a. 1959 returns—925 fish.
    b. 1960 returns—898 fish.
3. Returns of marked fall chinook to Little White Salmon Hatchery:

Mark*	Date released	*Fish returns in 1959*			*Fish returns in 1960*		
		Male	Female	Total	Male	Female	Total
		No.	*No.*	*No.*	*No.*	*No.*	*No.*
LP	May 8-9 (1957, 1958)	10	3	13	12	6	18
RP	July 1-2 (1957, 1958)	27	6	33	28	18	46
D-LP	Sept. 4 (1957, 1958)	3	....	3	4	2	6
D-RP	Oct. 15 (1957, 1958)	6	1	7	2	2	4
An-RP	Oct. 15 (1957, 1958)	20	....	20	20	11	31
An-LP	Feb. 13-15 (1958, 1959)	43	10	53	48	24	72
Total	....	109	20	129	114	63	177

*L=left; P=pectoral; R=right; D=dorsal; An=anal.

4. Returns of unmarked spring chinook to Carson National Fish Hatchery: Samples of several hundred scales (one from each fish) each year collected during 1955–57 and 1959–60.

In addition to the above impressions of scales of adult chinooks, specimens of young fall chinook, preserved at the time of release at several Federal hatcheries, were also available. Scales from these young fish were studied for comparison with the nuclear zone of adult scales.

The study was based on objective means as much as possible. Scales were studied under a microprojector at magnifications of 92, 140, or 400 times, depending on the magnification desired. The image of a scale was projected directly on millimeter graph paper, and the positions of circuli along the antero-lateral radius of the scale were marked on the paper. The center of the central plate was always used as the starting point, and the edge of the central plate became the first mark. In counting and measuring the circuli, we regarded the mark next to the central plate as the first circulus.

All subsequent studies of the scale growth were made from the markings on the graph paper. Distances were measured in terms of millimeters, and the actual dimensions determined by the magnifications used. The various methods of counting, measuring, and graphing will be described under individual sections.

SCALE GROWTH IN FALL CHINOOK SALMON RELEASED AS FRY AND FINGERLINGS

Spring Creek Hatchery (fig. 1), a Federal installation located about 175 miles from the mouth of the Columbia River on the Washington side, produces primarily fall chinook salmon. In the past, young chinooks were released either as unfed fry during the first week of February or as fed fingerlings during the first week of May. To evaluate the relative merits of fry and fingerling releases, the Bureau of Commercial Fisheries marked young chinook salmon of brood years 1956, 1957, and 1958. Among the young released each year during 1957–59, some fish were marked, consisting of about equal numbers of fry and fingerlings. Two combinations of fin marks were used: adipose and left pectoral fins on fry and adipose and right pectoral on fingerlings.

Fish with both marks were recovered in years 1958–60,[5] and scales were collected from all returned fish. An interesting question here is: "Can the scales of adults that were released as fry be differentiated from those that were released as fingerlings?" This problem is of both theoretical and practical importance.

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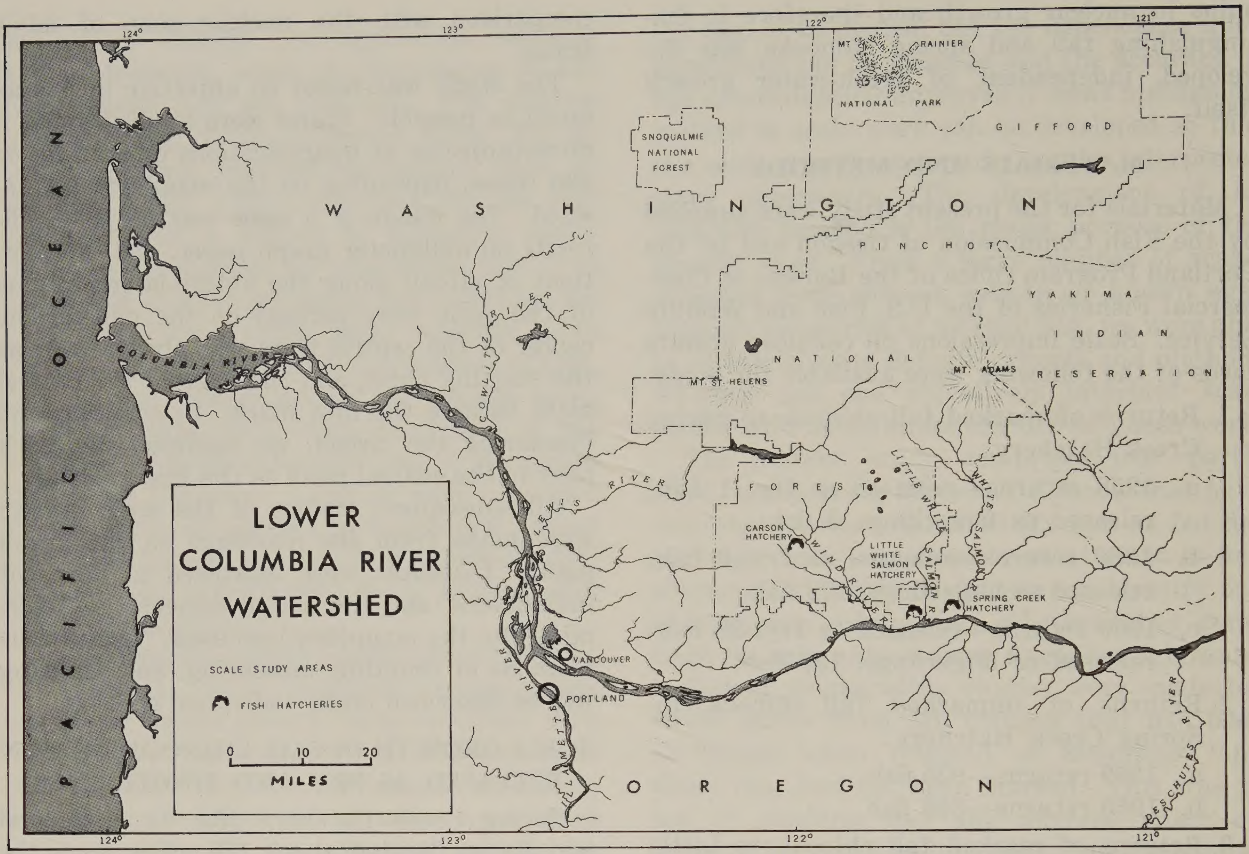
[5] Later recoveries are not included in the present study.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WASHINGTON
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SNOQUALMIE NATIONAL FOREST
GIFFORD PINCHOT NATIONAL FOREST
YAKIMA INDIAN RESERVATION
MT. ST. HELENS
MT. ADAMS
COLUMBIA RIVER
COWLITZ RIVER
LEWIS RIVER
WIND RIVER
LITTLE WHITE SALMON R.
WHITE SALMON R.
WILLAMETTE RIVER
DESCHUTES RIVER
CARSON HATCHERY
LITTLE WHITE SALMON HATCHERY
SPRING CREEK HATCHERY
VANCOUVER
PORTLAND

FIGURE 1.—Map of lower Columbia River watershed, showing locations of the three National Fish Hatcheries from which study materials were obtained.

Theoretically speaking, these two groups of fish should have differences in the growth pattern of scales, because at the time of release the fry have not started to grow scales, whereas the fingerlings have already grown scales with circuli. The nuclear area (the central portion of the scale), or at least the initial part of it, of adult scales originating from these two groups of fish must have then grown under different conditions: that from the fry group in river water under lower but variable temperature[6] and feeding conditions, and that from the fingerling group in hatchery water with higher and nearly constant temperature[7] and ample food. It may be expected then that scales from fish released as fry should have more closely spaced circuli in the nuclear zone than those released as fingerlings. Further, because the fry were released 3 months before the fingerlings, they should reach the ocean earlier and consequently may have a different pattern of ocean growth than have the fingerlings.

Practically speaking, if the origin of release — whether fry or fingerling — of returning adults can be identified through scale characters, then the two methods of release can be evaluated without having to mark young fish. Junge and Phinney (1963) indicate that fish released as fingerlings have a much greater survival rate than have fish released as fry. Therefore, the elimination of marking would not only save the costs of marking but also eliminate any possible harm that marking may cause the fish.

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[6] Water temperatures of Columbia River at Bonneville Dam in February were 2.8–4.4°C. (1957); 6.1–8.3°C. (1958); 3.9–5.0°C. (1959). U.S. Army Corps of Engineers, Annual Fish Passage Reports.

[7] Water temperature in Spring Creek Hatchery is about 7.8°C. year-round.

To find out whether actual differences existed between scales of adult fish released as fry and those from adults released as fingerlings, we selected scale samples from brood year 1956 because that year had the largest number of specimens that were released as fry. Returns of fish released as fingerlings are plentiful for analyzing this group in any brood year.

In 1959, eight fall chinook salmon with Ad–LP mark (released as fry) were recaptured. Of these, seven were 3 years old and therefore came from 1956 brood. In 1960, 28 such marked chinooks were recaptured and 16 of these were 4 years old and of the 1956 brood. This total of 23 scales that belonged to the 1956 brood, plus 102 3-year-olds that were recaptured in 1959 with Ad–RP marks (released as fingerlings) and 167 4-year-olds that were recaptured in 1960 with the same mark, provide the samples for the following study.

Based on theoretical considerations given earlier, we used two purely objective methods aimed at detecting any difference these two groups of scales might have in growth in fresh water or the first year of growth in the sea.

The first objective method was that of comparing growth patterns revealed by scale graphs based on spacing of circuli. Under a magnification of 140 times, the circuli were marked along the antero-lateral radius on a millimeter graph paper. We then divided the radius into 20-mm. units and calculated the mean spacing of circuli of each unit. For each group of scales, the means of circulus spacing of a unit were summed and averaged to give the mean of the group. When the group means were plotted on the ordinate against the radius units on the abscissa, we obtained a scale graph which shows the growth pattern.

Figure 2 shows information on groups released as fry and as fingerlings.

The fresh-water growth part of figure 2 shows a similar pattern for the two groups, namely, circuli are wide at the start but rapidly narrow down; the extent of growth covers about the same distance on scale radius. Also, there is only a slight difference in the mean spacing of circuli. Such difference, as will be shown in the second method, is not statistically significant.

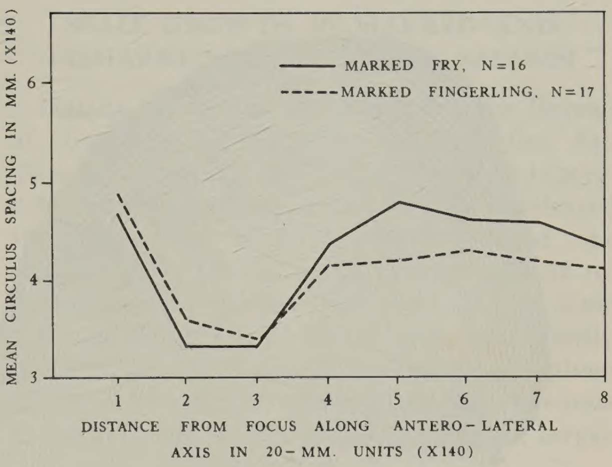

FIGURE 2

FIGURE 2.—Spring Creek Hatchery chinook salmon: Mean scale graphs showing pattern of fresh-water growth and the major portion of first year's marine growth of group marked as fry (solid line) and of group marked as fingerlings (dash line).

Marked difference, however, is evident in the marine growth section of figure 2 (units 4 to 8). The group released as fry has much wider circuli at every unit than has the group released as fingerlings. This is, of course, only a reflection of group difference, as the values plotted are mean widths. At each unit, the mean circulus widths of the two groups of scales overlap widely so that we could not identify the group origin of individual scales on that basis. Examples of scales of adults that were released as marked fry and as marked fingerlings are shown in figures 3 and 4.

The second objective method, aimed at detecting differences in first year growth of fish released as fry and as fingerlings, was to measure and compare the total distance of the first 5 circuli, of the first 10 circuli, and of 10 circuli counted from the 16th through 25th circulus.

The reasons for the selection of these three measurements are as follows: Fish released as fingerlings have developed, in the hatchery, the first 5 circuli and most, if not all, of the first 10 circuli; but the fry that are released develop all circuli in the natural environment. We measured the first 5 and first 10 circuli, therefore, to detect differences in initial fresh-water growth. The third measurement, distance from the 16th through 25th circulus, was made to

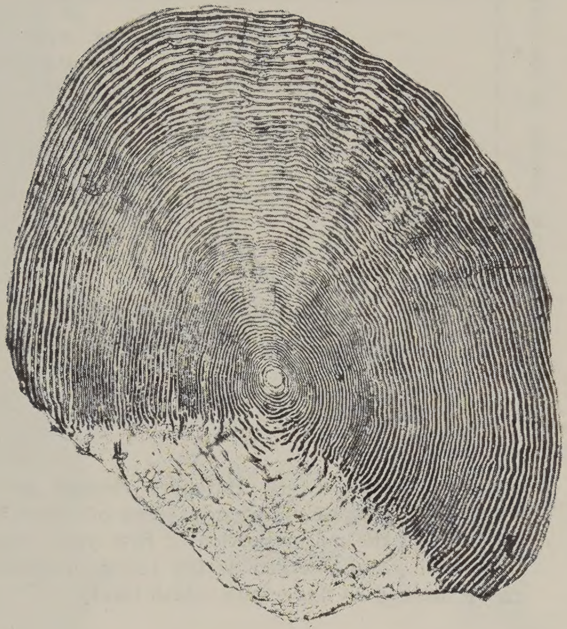

FIGURE 3.—A scale of Spring Creek Hatchery chinook salmon that was released as marked fry. Note the relatively wider spacing between circuli in the first year of marineg rowth.

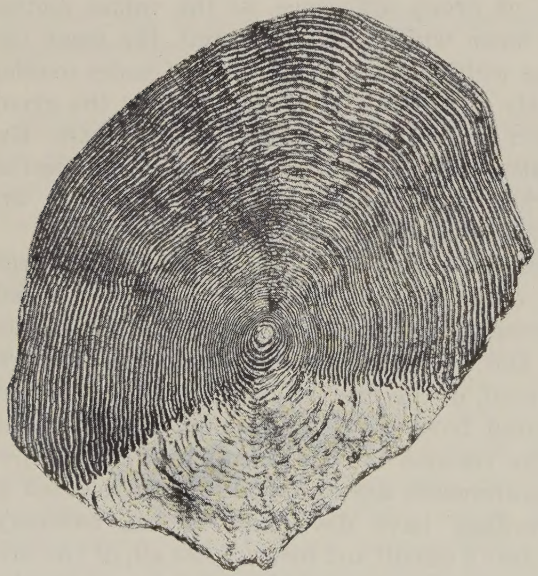

FIGURE 4.—A scale of Spring Creek Hatchery chinook salmon that was released as a marked fingerling. Note the relatively narrower spacing between circuli in the first year of marineg rowth.

study first-year marine growth, because these 10 circuli always represent the major but not the entire part of the first summer growth in the ocean. Using the 10 circuli enables us to have more consistent measurements than we would obtain by measuring the entire first summer growth, because we cannot delimit exactly the first and last circuli of summer growth. Circuli 11 through 15 were purposely skipped, for they may represent some transitional growth and therefore are quite variable as a group.

In reference to scale graphs, the initial 10 circuli are represented by the first two and a half units on the abscissa; and circuli 16 to 25, by units 4 to 6. In essence, the measuring method enables us to check on the graphing method, for we can tabulate the data and subject the results to statistical tests.

The results of the measurements and statistical tests are shown in table 1. In all the tests between the paired sample means, we first tested for the variances (s^2) and then applied the appropriate t-test.

In the comparisons of the first 5 circuli and of the first 10 circuli, the variances of the paired samples are significantly different, and t-test shows that the sample means are not significantly different. This is to say that although circulus spacing in the initial 5 or 10 circuli is more variable in the group released as fry (larger variance) than in the group released as fingerlings, the average values do not differ significantly between these two groups. The latter point confirms the results of the scale graph method

In the comparison of the 10 circuli counted from 16th to 25th circulus, the variances are not significantly different, and t-test shows that the sample mean of "A" (fry releases) is significantly larger than that of "B" (fingerling releases). This is to say that the groups released as fry and as fingerlings have a similar amount of variation in circulus spacing for circuli 16 to 25, but that the average spacing of circuli in the group released as fry is larger than that in the group released as fingerlings. The latter point also confirms the results of the scale graph method.

TABLE 1.—*Frequency and statistics of total distance of circuli of two groups of scales from salmon returning to Spring Creek Hatchery: A—adult chinooks that were marked and released as fry; B—adult chinooks that were marked and released as fingerlings*

Distance	First 5 circuli		First 10 circuli		Circuli 16–25	
	A	B	A	B	A	B
Mm. x 140	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
12–14		2				
14–16	6	12				
16–18	5	66				
18–20	6	70				
20–22	0	74				
22–24	4	31	1			
24–26	1	10		1		2
26–28	1	3		3		1
28–30		1	4	14	1	9
30–32			4	22	1	13
32–34			5	47	2	36
34–36			2	57	1	41
36–38			1	47	5	45
38–40			1	43	3	36
40–42			2	22	1	35
42–44			1	7	3	24
44–46			2	4	2	14
46–48				1	3	10
48–50				1		
50–52					1	2
52–54						
54–56						1
N	23	269	23	269	23	269
$\bar{x}$	18.8	19.6	34.3	35.8	39.8	37.7
s^2	12.69	6.94	32.58	14.97	32.63	23.12
95% confidence limits for ratio of population variances.	$1.09<\frac{s_A^2}{s_B^2}<3.66$		$1.31<\frac{s_A^2}{s_B^2}<4.36$		$0.84<\frac{s_A^2}{s_B^2}<2.82$	
t-statistic	−1.05		−1.24		2.10*	
d.f.	53		24		290	
Value of [*t*] at 0.05 significance level.	2.01		2.06		1.96	
95% confidence limits for difference between population means.	$-2.34<\mu_1-\mu_2<0.74$		$-3.99<\mu_1-\mu_2<0.99$		$0.14<\mu_1-\mu_2<4.01$	

That the variances of circulus spacing in both the first 5 circuli and the first 10 circuli are significantly greater for the fry-released group than for the fingerling-released group is as we expected, because the fry group grows the first 5 to 10 circuli in the river or estuary, where food and temperature conditions can be highly variable, while the fingerling group grows these same circuli in the hatchery, where the conditions are fairly uniform. Both groups form circuli 16 to 25 in the ocean, which explains why there is no significant difference between the two variances. Why the group released as fry grows more widely spaced circuli than does the group released as fingerlings is not understood. Perhaps it is due to the earlier entry into the ocean by the fry.

SCALE GROWTH IN MARKED AND UNMARKED FALL CHINOOK SALMON

During the 3 years 1957–59 when the Bureau of Commercial Fisheries marked the fall chinook salmon at the Spring Creek Hatchery, both marked and unmarked fish were released simultaneously. When the fish returned, the unmarked fish had a much greater rate of return than the marked fish. Also, at the same age the unmarked chinook were consistently larger than the marked. Examples are given in figure 5 in which the modal length of female unmarked fish is 2 inches, or 6 percent, larger than that of female marked fish, which had their adipose and right pectoral removed. Male chinook salmon exhibited similar differences.

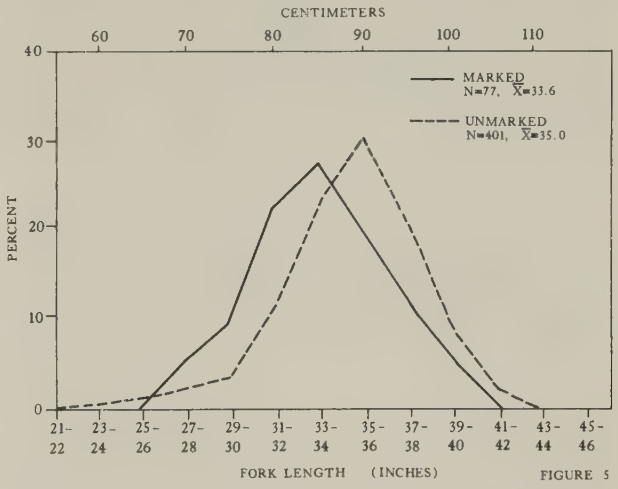

FIGURE 5.—Size frequencies of female 4-year-old Spring Creek Hatchery marked and unmarked chinooks that were released as fingerlings (1956 brood) returned in 1960.

To see if the difference in size between returns of marked and unmarked chinook is manifested in scale growth, we studied the returns of 4-year-old females in 1960. We first compared scales from fish of modal length in each group (33–34 inches in the marked group and 35–36 inches in the unmarked group). Then, we studied unmarked fish 33 to 34 inches long. To do this objectively, we constructed and compared mean scale graphs showing circulus spacing and growth pattern. Of the marked fish returns, only the group released as fingerlings were studied for very few returns were available from fish released as fry.

The three mean scale graphs for the marked and unmarked female fall chinook salmon that returned to the Spring Creek Hatchery in 1960 as 4-year-olds are shown in figure 6. These graphs show the growth period from the beginning of scale growth toward the end of the first summer in the ocean. They represent, therefore, only part of the antero-lateral radius. The initial part of the graphs (units 1–4), which represents fresh-water and intermediate growth, is very similar among the three groups. The remaining part of the graphs (units 5–8), which represents the major part of first marine growth, becomes divergent in that the mean circulus spacing of the marked group is consistently smaller than that of either of the two unmarked groups (33–34 inches, 35–36 inches), with greater difference shown between the marked and the larger unmarked fish.

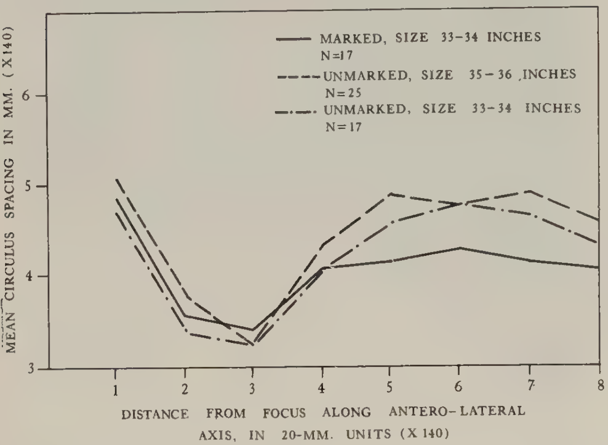

FIGURE 6

FIGURE 6.—Mean scale graphs of marked and unmarked female fall chinooks of three selected size groups that returned to Spring Creek Hatchery in 1960 as 4-year-old fish.

The fact that the initial part of the scale graphs is similar among the three groups of chinook salmon is easily understood, because marking is applied during the fingerling stage after the fish have grown the initial part of the scale. The difference in the remaining part of the scale graphs between the marked and unmarked groups, especially between those of the same size, strongly suggests that marking has slowed down the fish's growth rate, at least during the first summer in the ocean.

To verify the results revealed by the scale graphs, the total distance from the 16th to 25th circulus, which represents the major part of the first year's marine growth, was measured and a *t*-test applied (table 2). We first tested sample variances, and in both pairs equality can be accepted; therefore, a simple *t*-test was used. The width of ten marine circuli was significantly greater in the unmarked groups than in the marked group, compared either between two modal lengths of fish or between fish of the same length. These tests thus confirm the results obtained by the scale graph method.

TABLE 2.—*Frequency and statistics of measurements of scale growth during first year's marine life in marked and unmarked fall chinook salmon that returned in 1960 to Spring Creek Hatchery as 4-year-olds*

Distance of 10 circuli (16th–25th)	Marked fish 33–34 inches long	Unmarked fish 33–34 inches long	Marked fish 33–34 inches long	Unmarked fish 35–36 inches long
	A	B	A	B
Mm. x 140	*Number*	*Number*	*Number*	*Number*
31	1		1	
32	0		0	
33	0		0	
34	1		1	
35	0		0	
36	1	1	1	
37	2	0	2	
38	2	0	2	1
39	1	0	1	0
40	0	2	0	0
41	2	1	2	4
42	0	1	0	0
43	1	1	1	2
44	3	2	3	1
45	0	2	0	2
46	1	0	1	0
47	0	1	0	3
48	0	0	0	1
49	0	0	0	1
50	0	2	0	4
51	2	2	2	1
52		2		3
53				1
54				1
55				1
N	17	17	17	26
$\bar{x}$	40.88	45.47	40.88	47.27
s^2	30.23	23.89	30.23	22.12
95 percent confidence limits for ratio of population variances.	$0.29<\frac{s_A^2}{s_B^2}<2.19$		$0.28<\frac{s_A^2}{s_B^2}<1.74$	
t-statistic	−3.58*		4.12*	
d.f.	32		41	
Value of [*t*] at 0.05 significance level.	2.04		2.02	
95 percent confidence limits for difference between population means.	$-9.95<\mu_1-\mu_2<-2.73$		$3.25<\mu_1-\mu_2<9.53$	

Growth rates of fishes are reflected in the spacing of scale circuli: the faster the growth rate, the wider the spacing between circuli. The present findings, therefore, suggest that marking through the excision of adipose and right pectoral fins in chinook salmon may have been responsible for the slower growth rate of the marked fish. Biologists, using various fin marks, working on various species of fish, and experimenting under various conditions, have obtained contradictory results in this respect. Ricker (1949), for instance, excised the pectoral, both ventrals, or one pectoral and both ventrals of the largemouth bass and found that recoveries of these and unmarked fish indicated that the marked fish were significantly smaller than the unmarked ones. He believes that marking possibly affected the growth rate directly; however, when he marked 2-year-old bluegills, the growth of marked and unmarked fish was the same. Armstrong (1949) studied lake trout fingerlings and found no appreciable difference in length and weight between those that were unmarked and those that had had the adipose removed. Shetter (1951) also shows that removal of the dorsal and adipose fins, right pectoral fin, or right pelvic fin from the fingerling lake trout had no effect on the growth of the marked fish but that removal of the left pectoral appeared to have slowed the growth of the fish. Again, on a study of growth of marked and unmarked lake trout fingerlings in the presence of predatory fish, Shetter (1952) found no significant difference in the growth rate between marked and unmarked groups.

In the Cultus Lake experiments on the sockeye salmon, Foerster (1934, 1936a, 1936b) shows that unmarked smolts had a return rate two and one-half times greater than marked smolts that had both pelvics and adipose or both pelvics and dorsal removed. He shows further that this differential mortality was due to the effect of marking upon marine survival, since marking did not affect lake survival. No data on fish length or scale growth were given, however, so it is not known whether marking did have an adverse effect on growth.

The reasons for the apparent paradoxical results on the effect of marking on the growth rate of fish by various workers may be quite varied. The different results could be due to different fins being clipped, different species being experimented on, different techniques being applied, or different conditions under which the experiments were made.

SCALE GROWTH OF FALL CHINOOK SALMON, RELEASED BETWEEN MAY AND FEBRUARY

At Little White Salmon Hatchery (fig. 1), another Federal installation some 10 miles downriver from the Spring Creek Hatchery, the Bureau of Commercial Fisheries has conducted further marking experiments on fall chinook salmon. Here, for the brood years 1956–58, young chinook salmon were reared for various lengths of time and released at five different times of the year from May to February (see under "Materials and Methods"). A different mark was applied for each release, so that at return a marked fish could be positively identified as to its date of release.

The returns from these experiments offer excellent scale samples for studying the growth of nuclear zones. Fish released earliest (May) should go to sea during the first year, and their scales should show a typical ocean nucleus. Those released latest (February of the following year) spent the first winter in the hatchery, and their scales should therefore have a stream nucleus. Fish released between the above pe-

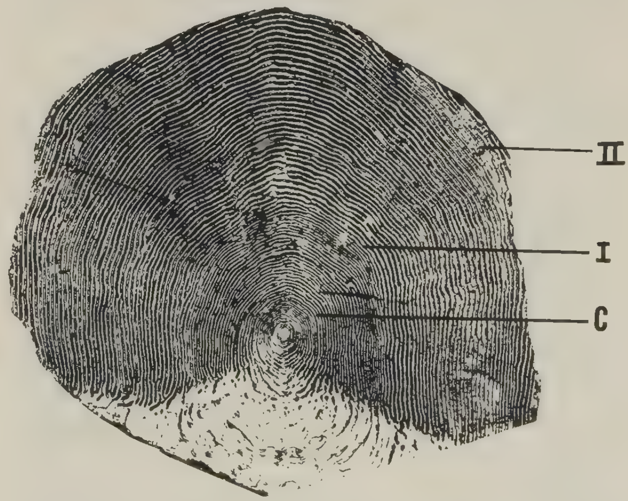

FIGURE 7.—A scale of adult chinook salmon that was released as a fingerling in May at the Little White Salmon Hatchery (May 1957 release, 1959 return).

riods (July, September, and October) should have scale growth of intermediate nature.

First, let us examine a typical scale of an adult chinook that originated from May release (fig. 7). At the center of the scale, there are 14 closely placed fine circuli, which are followed by more widely spaced coarser circuli. A check-like structure (C) is present at the border between the two zones. Most of the fine circuli represent intermediate growth that took place after the fish was released, because young chinook released in May average only two to three circuli on their scales. The zone of more widely spaced coarser circuli that follows the check represents what is generally regarded as marine growth. It is bounded by a distinct band of closely placed circuli (fig. 7, I). Both the check (C) and the band (I) have the appearance of an annulus. But since this is known to be an age II fish (1957 release, 1959 returns), and since the second annulus (II) is evident near the resorbed margin of the scale, only one of the two marks can be regarded as a genuine annulus. Based on relative distance, the band (I) should be regarded as the first annulus. "C," therefore, is a sort of migration check. The entire growth up to and including the band (I), forms what is known as the ocean nucleus. In the ocean nucleus, then, an annulus in the fresh-water growth part is lacking, and that gives rise to the age terminology of "sub-one" for this group,[8] or "O.", to use the terminology of Koo (1962).

Next, let us examine a tipical scale of an adult chinook that returned in 1960 from a February 1958 release (fig. 8). Here, there is also the central crowded area of fine circuli (I) and the surrounding wide marine growth that is bounded by a band of closely placed narrow circuli (II). Although "I" and "II" in this figure appear to be corresponding respectively to "C" and "I" in figure 7, they are different in significance. Because the fish was held in the hatchery over the winter and was not released until February, "I" in figure 8 is a true annulus, not a mere check, as the "C" in figure 7. The central area up to "I" forms what is known as the stream nucleus and because the young fish

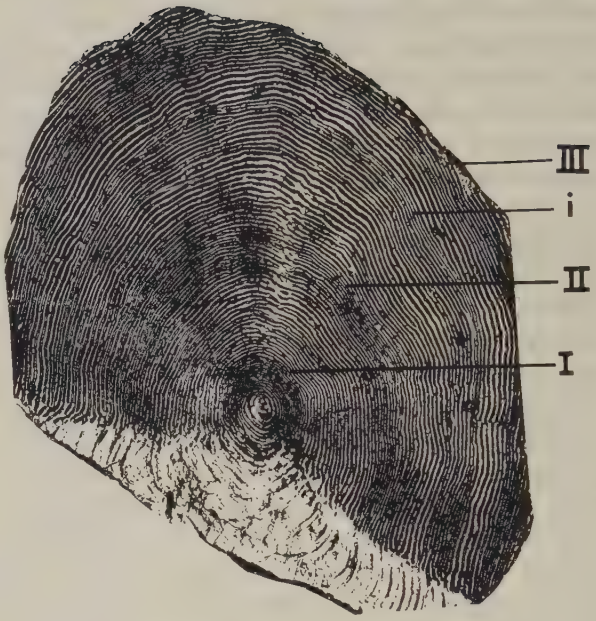

FIGURE 8.—A scale of adult chinook salmon that was released as a fingerling in February at the Little White Salmon Hatchery (February 1958 release, 1960 return).

left fresh water during its second year, it is also referred to as "sub-two age," or "1.", meaning one annulus in fresh-water growth. This fish is known to be age III, so there can be only two marine annuli, which are labeled as II and III in figure 8. The narrow band (i) between these two annuli must therefore be regarded as an incidental check.

From the standpoint of age determination, it is imperative that an ocean nucleus and a stream nucleus can be positively identified, for it will make a difference of 1 year in age, depending upon whether an annulus or a check is assigned to the central fine circuli area. No definite criteria can be found in literature that positively differentiate a mere check from a genuine annulus in this nuclear area of growth in chinook scales. Determination of age is usually based on the appearance of the nuclear zone and is highly dependent upon personal judgment. Thus, a stream nucleus has been described as an area of many closely placed circuli bounded by a distinct narrow band of more closely spaced circuli, the annulus. An ocean nucleus, on the other hand, is recognized when the nuclear zone consists of relatively few but wider circuli that are not marked off by a distinct check from the ensuing widely spaced marine growth.

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[8] The term "sub-one" is derived from the subscript of Gilbert-Rich's (1927) scale formula, for example, 3_1, 4_1.

Unfortunately, nuclear zones of many chinook salmon scales are not clearly defined so that the morphology of the nuclear zones alone does not enable us always to differentiate with certainty the ocean nuclei from the stream nuclei. If, for example, the scales in figures 7 and 8 had come from fish of unknown age, we would have no real basis for calling one mark a mere check (C) and the other a true annulus (I).

Obviously, something other than visual determination must be devised. As we had available a large number of scale samples from recaptured marked chinook salmon comprising both the stream type and the ocean type of nuclear growth, we were able to compare the characters of these two groups of scales on a quantitative basis. Because the nuclear zones of circuli failed to show significant differences, our study was extended to cover marine growth as well, and we have developed some criteria that help to guide the chinook scale reader to differentiate ocean from stream nuclei on a more objective basis.

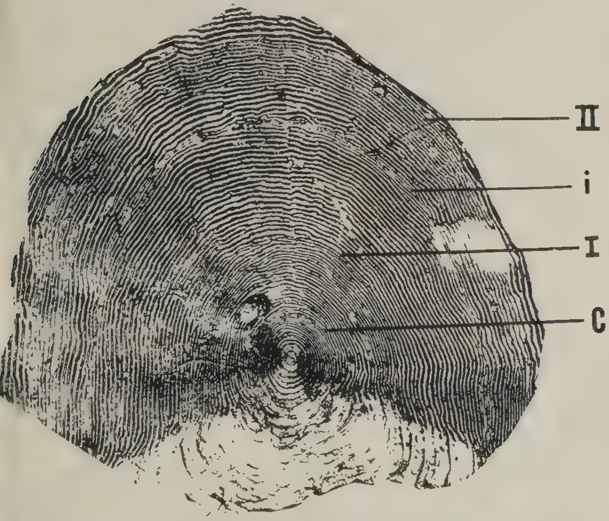

FIGURE 9.—A scale of adult chinook salmon that was released as a fingerling in July at the Little White Salmon Hatchery (July 1957 release, 1959 return.

Before we discuss quantitative measurements, let us examine some scales of adult chinook that originated from releases during the intermediate period between May of the first year and February of the next year, to observe the transition from ocean nucleus growth type to stream nucleus growth type.

A scale of a July release origin is shown in figure 9. Being similar to the scale of a May release origin (fig. 7), it also shows an ocean nucleus (I) and a strong check (C) for the nuclear area. Based on the known age of this

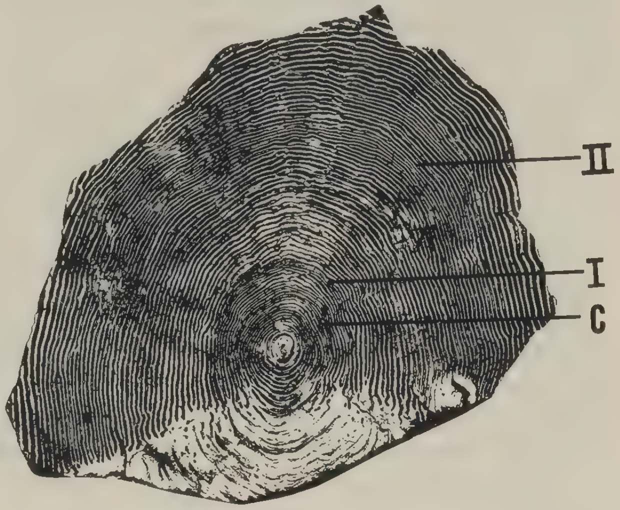

FIGURE 10.—A scale of adult chinook salmon that was released as a fingerling in September at the Little White Salmon Hatchery (September 1958 release, 1960 return).

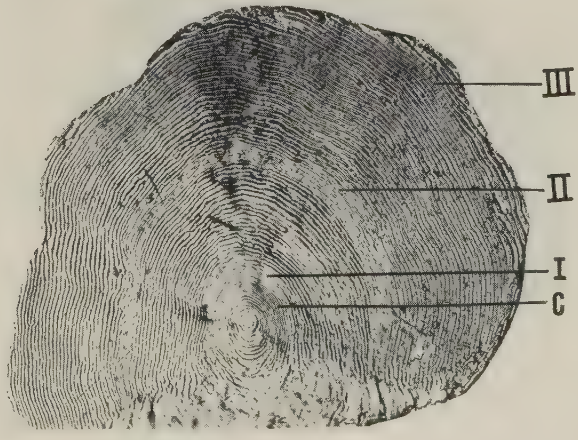

FIGURE 11.—A scale of adult chinook salmon that was released as a fingerling in September at the Little White Salmon Hatchery (September 1957 release, 1960 return).

fish, we know that "I" marks an annulus and "C" is merely a check. An incidental check (i) is also present between annuli I and II.

Two scales of adults that came from September release are shown in figures 10 and 11. In figure 10, the marine growth of the first year (C to I) is much reduced as compared with the scale of May or July release origin (figs. 7 and 9). Consequently, the annulus (I) is getting closer to the check (C), and the entire ocean nucleus becomes much smaller in size. Because of this, it is easy to determine that the check (C) here is not an annulus. Further reduction in the first year's marine growth is seen in the second example of a September release (fig. 11). Here the entire nuclear zone assumes the appearance of a stream nucleus. Indeed, it is questionable whether there is any amount of true marine growth inside the first annulus (I).

A scale of the October release origin (fig. 12) shows the same characteristics, i.e., a much reduced zone between "C" and "I," and a nuclear zone that assumes the look of a stream nucleus. At least, as far as age determination is concerned, because the total age of this fish is known to be III, it is certain that "I" is the first and only annulus up to that point, much as "I" in a typical stream nucleus such as that of a February release origin (fig. 8).

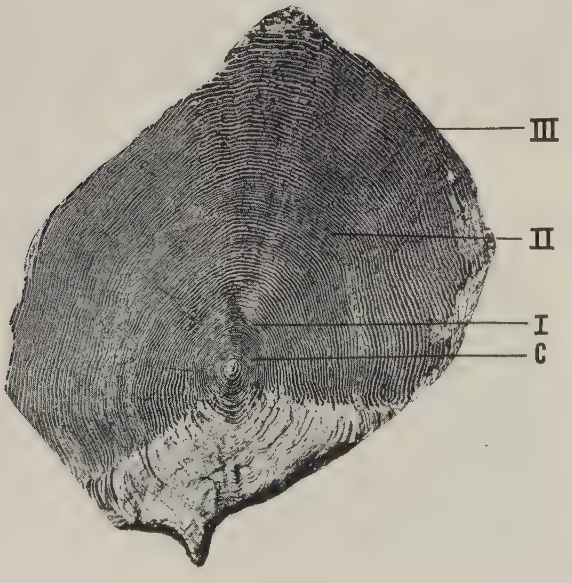

FIGURE 12.—A scale of adult chinook salmon that was released as a fingerling in October at the Little White Salmon Hatchery (October 1957 release, 1960 return).

From the above series of examples, it is evident that when the young chinook salmon were released as hatch-of-the-year from May through July, they entered the ocean during the growing season of the first year after some sojourn in the river. As a result, there was a large number of wide marine circuli outside the central zone of narrow fresh-water circuli, resulting in a large ocean nucleus. As the release date became later and later in the year (September and October), however, the chinook salmon would miss more and more of the current season's marine growth, and the result was a nuclear type similar in appearance to a stream nucleus. Finally, when the young chinook salmon were reared in fresh water over winter and were not released until February of the second year, the nuclear zone was composed solely of fresh-water growth, and any marine growth belonged to the following year. For all practical purposes, scales from September and October releases should be treated as stream nucleus type, for there is no way of knowing that "I" is not a stream annulus without the knowledge of release date.

Because the fresh-water growth part in an ocean nucleus may not be distinguishable from that of a stream nucleus, we extended our study into the marine growth of the first and second years of ocean life to find differences between these two types. In this study, 72 returns from May and July releases were treated as one group representing the ocean nucleus type, and 85 returns from October and February releases were treated as another group representing the stream nucleus type.

The method consists of first locating the apparent first marine annulus, i.e., a band of narrow circuli after a zone of wide circuli. This is "I" in figures 7 and 9 and "II" in figures 8, 11, and 12. Then, from the midpoint of this annulus band 20 circuli were counted outward toward the edge of the scale along an antero-lateral radius, and the total distance of these 20 circuli was measured and represented by "A." This represents the major part of the second year growth in ocean for both groups of scales. Similarly, 20 circuli were counted inward toward the focus and the total distance was measured as "B" (fig. 13), which represents the first year growth in ocean for both groups of scales. Then we computed the ratio of A/B, which is the ratio of second year marine growth to the first year marine growth.

We found that in the May to July release group, circuli of the second year marine growth (A) were, on the average, nearly 50 percent wider than the first year marine growth (B); whereas in the October to February release group, "A" was only 22 percent wider than "B". The frequency distribution of the ratio A/B of these two groups of scales is shown in figure 14. It is obvious that the two groups are distinctly different in the value of A/B, but there is also enough overlap so that not all scales can be identified to their nuclear growth type on this character alone.

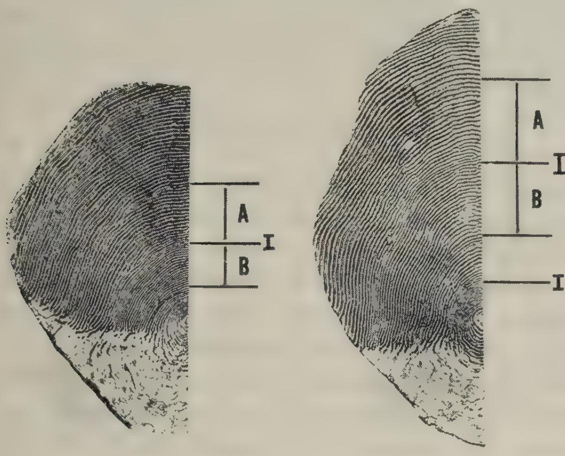

FIGURE 13.—The measurement of circulus spacing. Left, chinook scale with an ocean nucleus; right, chinook scale with a stream nucleus.

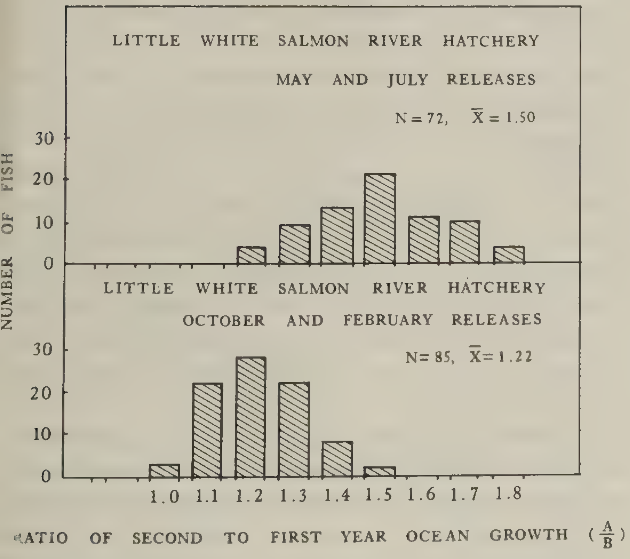

FIGURE 14

FIGURE 14.—Frequency distribution of the ratio of second to first year marine growth (A/B) of little white salmon Hatchery recaptures of May and July releases, and October and February releases.

DIFFERENTIATION OF FALL CHINOOK AND SPRING CHINOOK SCALES BY MARINE GROWTH

The fall chinook scales normally have a typical ocean nucleus (sub-one age), and the spring chinook scales normally have a typical stream nucleus (sub-two age). The nuclear growth part of these two types of scales cannot always be distinguished. So in order to identify these two groups of fish, we applied the method of comparing first and second year's marine

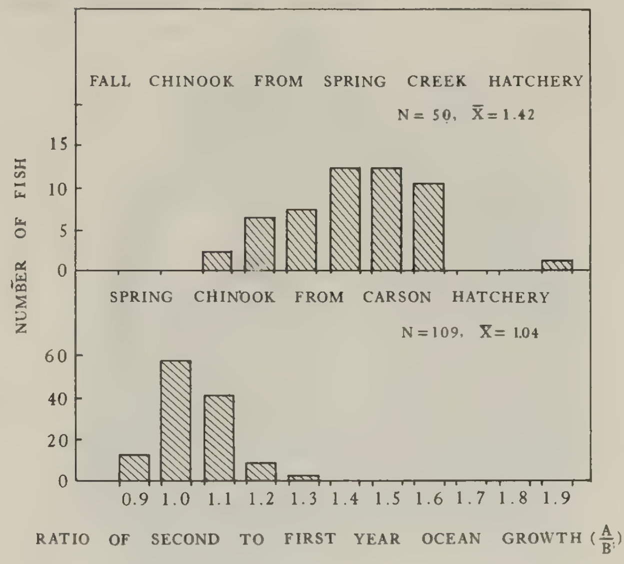

FIGURE 15

FIGURE 15.—Frequency distribution of the ratio of second to first year's marine growth (—A/B) of fall chinook and spring chinook.

growth as developed from the study of Little White Salmon Hatchery mark recovery specimens. For study material, we used scales collected from unmarked fall chinook at Spring Creek Hatchery and those collected from unmarked spring chinook at Carson Hatchery.

Scales of 50 fall chinook and 109 spring chinook were measured. The frequency distributions of the ratio of second year's to first year's marine growth A/B of these two groups of fish are shown in figure 15. These distributions show clearly that fall and spring chinooks are distinctly separate groups as far as the character of marine growth is concerned. The difference between the two groups is similar to that between May to July release group and October to February release group of Little White Salmon Hatchery fall chinook. In other words, the fall chinook are similar to May to July release group in having a large A/B ratio, and the spring chinook are similar to October to February release group of fall chinook in having a small A/B ratio.

The outstanding feature of spring chinook scales is that the marine growth of the first year is nearly as good as that of the second year, so that its A/B ratio approximates 1.0, as compared with 1.2 for the fall chinook released in October to February. In fact, this character alone is often sufficient to distinguish a spring run from a fall run of chinook salmon. An example of a spring chinook scale is shown in figure 16, in which the circuli inside of the first marine annulus (II) are as widely spaced as circuli outside of it.

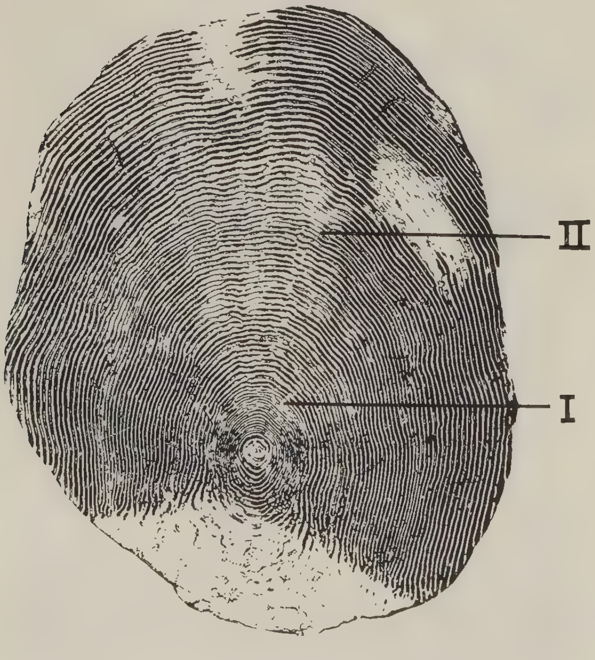

FIGURE 16.—A scale of a spring chinook salmon.

SUMMARY AND CONCLUSIONS

Scales of Columbia River chinook salmon were studied to find answers to the following questions:

1. Is it possible, from structures of adult chinook scales, to identify whether a fish has originated from fry or fingerling migrant?

The answer is negative. Scales from marked fish recoveries showed that there was no significant difference in the mean values of circulus spacing in nuclear growth part between chinook salmon released as fry and those released as fingerlings, although the spacing is more variable in the fry than in the fingerling group. In the first marine growth, circuli in the group released as fry are more widely spaced than in the group released as fingerlings. While the difference is statistically significant, there was too much overlap so that identification of individual scales was not possible.

2. Can the effect of marking, if any, on growth of chinook salmon be detected by scale studies?

The answer is positive. At the Spring Creek Hatchery, fall chinook fingerlings were marked by removal of adipose and right pectoral fins. When scales from marked fish recoveries were compared with those from unmarked fish returns, circulus spacing in marine growth of the marked group was found narrower than the unmarked group.

3. How do the scales of early season (May-July) releases of fall chinook differ from those of later season (October-February) releases?

In answering the above question, we found some interesting relations between scale growth patterns and times of release. Early season releases of fall chinook resulted in an ocean nucleus type (sub-one age) that is typical of fall chinook scales. Late season releases, however, resulted in a stream nucleus type (sub-two age) resembling that of spring chinook scales. Moreover, these two groups of scales are different in marine growth patterns. When circulus spacing in the second year marine growth is compared with that in the first year marine growth, the ratio is far greater for the sub-one group than for the sub-two group.

4. Can fall chinook scales be separated from spring chinook scales by objective means?

The answer is positive. Fall and spring chinooks can be differentiated by their scales. Differentiation, however, is not made from nuclear growth patterns as is usually done visually, but is achieved objectively by comparing marine growth circuli of the first 2 years, the same technique as used for early-season and late-season releases of fall chinook. In the spring chinook, circuli in the second year of marine growth are nearly 50 percent more widely spaced than those in the first year; whereas in the fall chinook, they are about the same.

ACKNOWLEDGMENTS

The most important ground work in connection with the present paper had been done before we started our studies, for marking experiments on the Columbia River chinook salmon and collecting scale samples and pertinent data had been performed by the Bureau of Commercial Fisheries of the U.S. Fish and Wildlife Service. Paul Zimmer, Harlan E. Johnson, and Roy Wahle of the Bureau provided the study material and data. The Fish Commission of Oregon and the Washington State Department of Fisheries, which are also studying the Columbia River chinook salmon, supplied additional material and information, and in this connection, I was assisted by Sigurd J. Westrheim, Raymond A. Willis, and Robert N. Thompson of the former organization and Peter Bergman of the latter agency. Charles E. Walker of the Canadian Department of Fisheries in Vancouver, British Columbia, sent us some duplicate scale impressions of Big Qualicum chinook salmon for our study, and Gerald J. Paulik of the Fisheries Research Institute of the University of Washington advised us on the statistical treatment of the data.

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CATCH AND ESTIMATES OF FISHING EFFORT AND APPARENT ABUNDANCE IN THE FISHERY FOR SKIPJACK TUNA (*KATSUWONUS PELAMIS*) IN HAWAIIAN WATERS, 1952–62

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ABSTRACT

Detailed data on catch and effort are obtained each year from all vessels that fish full time in the Hawaiian skipjack tuna fleet. These data permit description of the fishery and inferences about the abundance of skipjack. Our past measures of abundance have been stated in terms of total catch and catch per unit of effort calculated in terms of productive trips of all sizes of vessel. This study offers information on changes in the apparent abundance of skipjack in Hawaiian waters calculated from standardized units that will be unaffected by changes in the numbers of small and large vessels in the fishing fleet.

Effort was measured in terms of an "effective" trip, which was defined as a trip in which skipjack were caught. Bias introduced by the lack of data on zero-catch trips is discussed.

The number of men hooking per trip declined in 1950–60; however, those that remained in the fishery increased their catch rate by shifting their emphasis in fishing technique from "grasping and unhooking" each fish to "flipping," a method in which the fisherman swings the fish aboard and by relaxing the tension on the pole, permits the hook to fall clear of the fish's mouth. The higher catch rate from the "flipping" method was one of the factors that offset the effect of the decline in the number of men. Another factor that appeared to increase the catch rate was the reduction in the number of small vessels that did poorly.

The vessels were separated into two size classes: Class 1, with bait-carrying capacities of less than 800 gallons per baitwell; Class 2, with bait capacities of more than 800 gallons per baitwell.

The catch was standardized to Class 2 vessels. The catch per standard effective trip (Y/f) and the total catch fluctuated similarly in all years. The Y/f had no apparent trend and averaged about 5,700 pounds. The Y/f and the relative effective fishing intensity were not correlated significantly over the 11-year period. Year-to-year changes in apparent abundance seem to be independent of changes in fishing effort.

I concluded that variations in the availability and vulnerability of skipjack contribute to fluctuations in landings. The variations in strength of year classes also may have contributed importantly to fluctuations in the landings.

In Hawaii, the skipjack tuna, *Katsuwonus pelamis* (Linnaeus), or aku, as it is called locally, supports the State's most important commercial fishery, contributing about 66 percent by weight to the total Hawaiian marine catch, and accounting for about 40 percent of the total annual ex-vessel value. The fish are caught exclusively by pole and line from schools which are concentrated at the stern of the vessel by chumming with live bait. The fishery is highly seasonal. Landings have ranged from about 29,000 pounds in January, typically a poor month, to about 3.7 million pounds in July, when the catch usually is large. Four- to 5-pound fish usually are caught throughout the year, but between May and September, larger fish, ranging between 13 and 25 pounds, are also taken. The latter contribute a large percentage by weight to the total annual catch. Not only does the catch fluctuate by month but also by year. In 1952–62, the yearly landings ranged between 6.1 and 14.0 million pounds, apparently with changes in the numbers of the larger fish at the islands.

In the past, abundance of skipjack tuna in Hawaiian waters has been measured in terms of total catch and catch per unit of effort calculated in productive trips of all sizes of vessels —uncorrected fishing effort (Yamashita, 1958; Shippen, 1961). In general, total catch is not a dependable measure of abundance, because it is affected seriously by changes in the amount

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of fishing effort and by weather and sea conditions. Catch per unit of effort calculated in terms of uncorrected fishing effort is also unreliable because it varies from year to year with changes in the fishing fleet. The fleet is made up of vessels of different sizes, and numbers of these change as some enter and some leave the fishery. Both size and number affect the catch per unit of effort. An important phase of this study is the derivation of a measure of abundance of skipjack in Hawaiian waters based on catch per unit of effort in standardized units that are unaffected by changes in the fishing fleet.

SOURCES OF MATERIALS

The basic data for this study were obtained from Fish Catch Reports (January 1952 to June 1954) and Aku Catch Reports (July 1954 to December 1962) submitted by the fishermen to the Hawaii Division of Fish and Game. Catch reports of only those vessels that fished for skipjack tuna full time were used. The report form has undergone several revisions through the years, but all versions have carried spaces for the following information: The date of landing, the pounds of skipjack caught, and the fishing area. Yamashita (1958) described the method of reporting the areas fished by a skipjack vessel. Briefly, a fisherman reports only the code number corresponding to the statistical area where the catch was made. These areas are indicated on the Division of Fish and Game's Fisheries Chart No. 2 (see Yamashita, 1958: fig. 2).

Data on number of men hooking per trip were obtained from Aku Boat Interview Sheets (January 1950 to July 1956), which were collected and checked by the personnel of the Division of Fish and Game, from logbook records (1957–59), and from Sampan Interview Records (August 1959 to June 1961).

DESCRIPTION OF THE FISHERY

The present brief description of the fishery and review of fishing operations is based on June (1951). The number of skipjack tuna sampans fishing full time reached a maximum of 28 in 1951, but since then has declined; in 1963 only 20 vessels were fishing full time for skipjack. The vessels, generally of wooden construction, range from 58.3 to 80.5 feet in registered length and from 27 to 77 in gross tonnage. These vessels carry 6 to 14 men per fishing trip.

The nehu or anchovy, *Stolephorus purpureus* Fowler, makes up about 92 percent of the bait catch; a second bait is the iao or silverside, *Pranesus insularum* (Jordan and Evermann). Each vessel catches its own bait, fishing day and night until a sufficient supply is obtained. All the vessels have six baitwells with screened holes at the bottom through which sea water circulates.

The Hawaiian skipjack tuna fishermen usually confine their fishing and scouting operations to waters within 90 miles of the main islands. Skipjack on the fishing ground are indicated to the fishermen almost exclusively by bird flocks which are often associated with schools of fish. When a school has been sighted the captain attempts to intercept it. Once the head of the school is reached, water sprays are turned on and the "chummer" scatters live bait into the water. If the skipjack bite, the fishermen begin fishing off the stern. Fishing continues until the bait supply is exhausted or until the captain decides that further fishing is not worthwhile. If chumming is unsuccessful, the school is abandoned and scouting is resumed. The sampans may encounter several skipjack tuna schools during the day, but the fish may bite in only about half of them. Scouting and fishing are discontinued as dark approaches, and the vessels usually head for port to unload the day's catch.

TRENDS IN CATCHES OF SKIPJACK TUNA

To show the trends in catches of skipjack tuna from Hawaiian waters, catch statistics were summarized by months and quarters for each year and by two broad geographical areas. Comments on the trends of catches are based on tabulation of data for 1952–62; therefore, the results may not be in complete agreement with those published for 1948–53 by Yamashita (1958).

TABLE 1.—*Monthly, quarterly, and annual catches of skipjack tuna in Hawaii, 1952–62*

[Thousands of pounds]

Period of time	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	Range	Average
Month:													
January	29	200	271	98	322	524	638	215	242	492	459	29–638	317
February	90	204	185	118	281	133	236	107	179	247	412	90–412	199
March	56	576	359	263	230	454	151	397	327	600	199	56–600	328
April	387	864	759	681	433	331	792	839	411	620	480	331–864	600
May	578	1,240	1,132	1,399	1,375	816	277	1,757	842	930	1,178	277–1,757	1,048
June	818	2,241	2,804	2,197	1,926	812	948	1,679	776	2,721	2,308	776–2,804	1,748
July	1,654	1,510	3,705	1,824	2,321	919	1,405	2,382	1,430	2,288	1,809	919–3,705	1,932
August	1,758	2,142	2,178	1,170	1,586	698	1,191	1,815	1,396	1,359	922	698–2,178	1,474
September	987	1,281	1,049	993	1,055	489	631	1,377	690	705	568	489–1,377	893
October	576	1,199	1,121	440	725	530	186	1,064	439	516	525	186–1,199	666
November	110	218	390	272	635	282	144	626	219	213	170	110–635	298
December	249	384	68	239	243	142	235	155	409	203	385	68–409	246
Quarter:													
First	175	980	815	479	833	1,111	1,025	719	748	1,339	1,070	175–1,339	845
Second	1,783	4,345	4,695	4,277	3,734	1,959	2,017	4,275	2,029	4,271	3,966	1,783–4,695	3,395
Third	4,399	4,933	6,932	3,987	4,962	2,106	3,227	5,574	3,516	4,352	3,299	2,106–6,932	4,299
Fourth	935	1,801	1,579	951	1,603	954	565	1,845	1,067	932	1,080	565–1,844	1,210
Annual	7,292	12,059	14,021	9,694	11,132	6,130	6,834	12,413	7,360	10,894	9,415	6,130–14,021	9,749

MONTHLY, QUARTERLY, AND ANNUAL CATCHES

The seasonal character of the Hawaiian skipjack tuna fishery is shown by the monthly and quarterly catches in 1952–62 (table 1). The catch usually increased gradually from April to a peak in June, July, or August and then declined progressively to a low level in December. Usually February had the smallest catch and July the largest. Also, the catch usually rose in January following the progressive decline from the summer peak to December.

The quarterly catches showed the same trend as the monthly landings. First-quarter catches were usually the smallest and averaged 0.8 million pounds. Second-quarter catches reflected the increased fishing activity during the spring and averaged about 3.4 million pounds. Third-quarter landings were rather consistently the largest and averaged 4.3 million pounds; only in 1955 and 1962 did second-quarter catches exceed those of the third quarter. The fourth-quarter catches declined to an average of 1.2 million pounds.

The variations of the annual catches were large. In 1952–62, there were 4 poor years—1952, 1957, 1958, and 1960—in which the catches were far below the 11-year average of 9.7 million pounds. The catches in 1955 and 1962 were close to the 11-year average, and those of the remaining years were above average. The maximum catch of 14.0 million pounds occurred in 1954; the minimum of 6.1 million pounds was in 1957.

INSHORE AND OFFSHORE CATCHES

For this study, I consider the inshore area to extend from the coastline to 20 miles at sea and the offshore area to include all statistical areas beyond 20 miles from the coastline.

The catch reports used in this study were from vessels that fished for skipjack full time. The total weight landed by these vessels and the effort expended to produce it are hereafter called sample catch and sample effort. In addition to the catches made by these vessels, catches were made by vessels that fished for skipjack tuna only part time. The total weight landed by vessels that fished full time and those that fished part time is hereafter called total catch and the effort expended to produce it is total effort. Data on total catch were obtained from annual summaries of catch issued by the Hawaii Division of Fish and Game.

I obtained the sample catch (all areas) and the sample inshore catch from the catch reports, and from these data, I calculated the percentage of the catch made inshore. The total inshore catch was estimated by applying the percentage of the catch made inshore to the total catch. The estimated annual inshore catches (table 2) are shown in relation to the total catch and the estimated total offshore catch in figure 1.

The percentage of the catch made inshore ranged from 63 percent in 1954 to 90 percent in 1960. During the poor years—1952, 1957, 1958, and 1960—the inshore catch averaged 83 percent of the total catch, whereas in

TABLE 2.—*Estimated total inshore and total offshore catches of skipjack tuna in Hawaiian waters, 1952–62*

Year	Sample catch all areas	Percentage of sample catch inshore	Actual total catch	Estimated inshore catch	Estimated offshore catch
	Thousand pounds	*Percent*	*Thousand pounds*	*Thousand pounds*	*Thousand pounds*
1952	6,277	76	7,292	5,542	1,750
1953	10,543	66	12,059	7,959	4,100
1954	11,229	63	14,021	8,833	5,188
1955	8,257	83	9,694	8,046	1,648
1956	10,937	73	11,132	8,126	3,006
1957	6,075	80	6,130	4,904	1,226
1958	6,494	86	6,834	5,877	957
1959	11,945	83	12,413	10,303	2,110
1960	7,107	90	7,360	6,624	736
1961	10,780	78	10,894	8,497	2,397
1962	9,086	82	9,415	7,720	1,695

average and good years the inshore catch averaged 75 percent.

Yamashita (1958) who examined the 1948–53 catches of skipjack tuna suggested that about 8.0 million pounds may be nearly the maximum that can be obtained in the inshore area. The present study indicates, however, that the inshore catch can be well above this level. The 1959 landings, for example, were 10.3 million pounds and were caught by a fleet of 21 full-time vessels, although in 1949–53 26 to 28 vessels were fishing full time for skipjack.

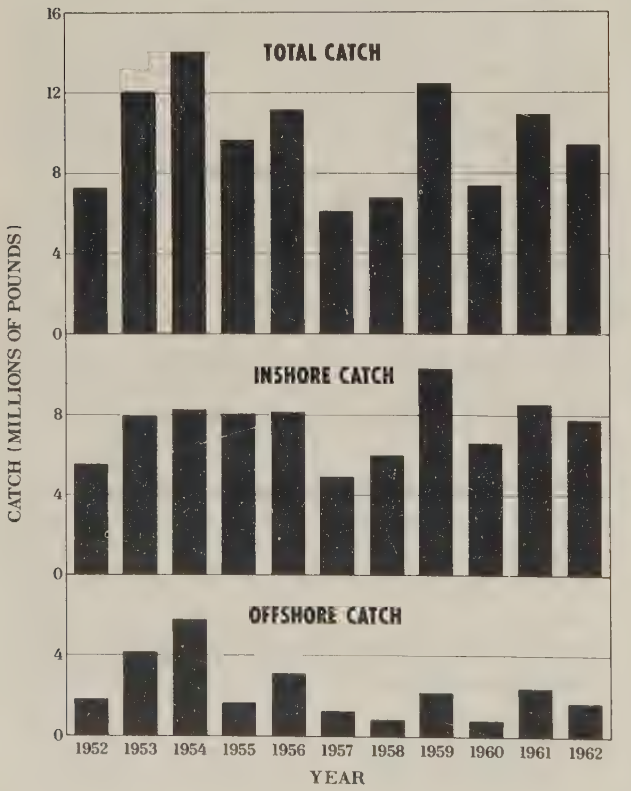

FIGURE 1.—Total catch of skipjack tuna (all areas) and the estimated inshore and offshore catches in the Hawaiian fishery, 1952-62.

The offshore catch increased gradually from 1.8 million pounds in 1952 to a peak of about 5.2 million pounds in 1954 (fig. 1). After a sharp decline to about 1.6 million pounds in the following year, the offshore take fluctuated between 0.8 and 3.0 million pounds from 1956 to 1962.

FISHING INTENSITY

Fishing intensity is the total amount of effort expended in catching fish. Effort changes with time in different ways. For example, in a fishery where a trip is considered a unit of fishing effort, an increase in the duration of trips or an increase in the fishing power of vessels alters the unit of effort. These changes complicate the analysis of catch and effort data; therefore it becomes necessary to obtain and examine information on size of vessels, on modification of or improvement to fishing gear, and on changes in fishing time.

SIZE CLASSES OF VESSELS

It may be expected that size of a vessel influences its potential efficiency as a fishing unit in a pole-and-line fishery because the larger crews give the larger vessels greater fishing power. One measure of effort is the number of men aboard per trip; this number may vary among vessels and with the years. The interview records for 1950–56 indicated that the number of men aboard per trip varied between 6 and 14.

The effects of this crew variability were reduced by separating the vessels arbitrarily into two size classes according to their bait-carrying capacities. The bait-carrying capacity was a good measure of the vessel's fish capacity, because on the return to port the empty baitwells were used to store the catch. The vessels with large bait capacities were the large ones that usually carried more men. Data on the bait capacity of most of the vessels in the fleet were given by Yamashita (1958; appendix table 1).

The bait capacity of a vessel is stated in terms of the average effective volume in gallons per baitwell and is derived from the length of the baitwell, its width, and its depth up to the water level.

The size classes of vessels used in this study are as follows:

Class 1.—Bait capacity up to 800 gallons per baitwell; registered length, 58.3 to 71.9 feet; gross tonnage, 27 to 54 tons; engine, 110 to 450 horsepower. Their number ranged from 8 to 16 in 1952–62.

Class 2.—Bait capacity more than 800 gallons per baitwell; registered length, 65.0 to 80.5 feet; gross tonnage, 45 to 77 tons; engine, 160 to 600 horsepower. Their number ranged from 11 to 14 in 1952–62.

It was necessary to estimate the bait-carrying capacity of four vessels for which Yamashita (1958) gave no records. To determine the most dependable procedure, characteristics such as gross tonnage, net tonnage, registered length, and engine horsepower, were examined in relation to average effective volume of baitwells. The regression of average effective volume per baitwell (*Y*) on gross tonnage (*X*) (fig. 2) proved to have the smallest error of estimate. This relation was used therefore, to estimate the average effective volume of the four vessels.

THE EFFECTIVE TRIP AS A MEASURE OF EFFORT

The records used carried three types of statistics from which one might estimate effort: The number of men hooking per trip, the number of men aboard per trip, and the number of trips. The number of men hooking per trip and the number of men aboard per trip were not consistently entered; therefore, I selected the number of fishing trips as the unit of effort. The catch reports showed all trips on which a catch was made, but gave no indication of zero-catch trips. For this study I define effort as an effective trip (a trip on which skipjack tuna were caught).

Because zero-catch trips were not recorded, effort always is underestimated. The extent of the underestimate may not be serious in some years, because zero-catch trips are fewer when fishing is good (Shippen, 1961). This source of error can weigh heavily, however, in a year of poor fishing, when zero-catch trips become numerous.

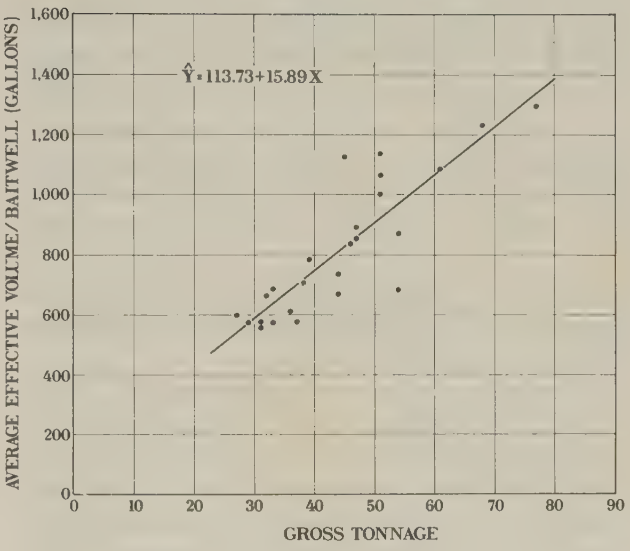

FIGURE 2.–Regression of average effective volume per baitwell on gross tonnage of Hawaiian skipjack tuna vessels.

ESTIMATES OF ZERO-CATCH TRIPS

Because only the number of effective trips is known from the catch reports, estimates of catch per effective trip (Y/g) are larger than if total effort had been used, assuming that zero-catch trips occur from time to time. (The notation Y refers to the total weight of fish in the catch and g to the fishing effort or effective trip as recorded. In a later section of this paper the notation f is used to refer to fishing effort expressed in standard effective trips.) A measure of effort, however, should reflect zero-catch trips as well as those on which fish were caught.

Logbook records available for a few vessels in 1957–59 provided some data on zero-catch trips (table 3). Five vessels kept logbooks in 1957, seven in 1958 and five in 1959; the vessels represented 20, 29, and 24 percent of the fleet.

TABLE 3.—*The total catch, number of Class 1 and Class 2 vessels sampled, their total recorded trips, and number and percentage of zero-catch trips, Hawaii, 1957–59*

Year	Total catch	Class 1				Class 2			
		Vessels	Trips	Zero-catch trips		Vessels	Trips	Zero-catch trips	
	Thousand pounds	*Number*	*Number*	*Number*	*Percent*	*Number*	*Number*	*Number*	*Percent*
1957	6,130	2	181	51	28	3	357	136	38
1958	6,834	2	145	31	21	5	482	131	27
1959	12,413	1	93	2	2	4	336	32	10

Because no additional data are available, I assumed that this sample represents the fleet's activities for these years.

Zero-catch trips were more frequent among Class 2 than among Class 1 vessels (table 3). The higher rate of occurrence in poor years (1957–58) than in the good year (1959) indicates that the percentage of zero-catch trips tends to decrease as total catch increases. The apparent negative correlation between these variables is supported to some extent by Shippen (1961: table 2) who analyzed the logbooks of two vessels. (The original records show that these were Class 2 vessels.) He found that in a poor year (1952), zero-catch trips accounted for 10 percent of the total trips made by Boat A and 14 percent of those made by Boat B. In a good year (1953), zero-catch trips were 8 and 10 percent for Boat A and Boat B, respectively.

The numbers of effective trips and zero-catch trips were used to estimate the total effort for 1957–59. For example, in 1957, the total number of zero-catch trips among Class 1 vessels was estimated by simple proportion to be 262. The estimated total effort for both size classes for 1957–59 is given in table 4.

TABLE 4.—*Number of effective trips and estimated number of zero-catch trips of Class 1 and Class 2 vessels, Hawaii, 1957–59*

Year	Vessels	Class 1			Class 2		
		Effective trips	Estimated zero-catch trips	Estimated total trips	Effective trips	Estimated zero-catch trips	Estimated total trips
	Number	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
1957	25	668	262	930	910	560	1,470
1958	24	659	179	838	865	323	1,188
1959	21	779	17	796	1,055	111	1,166

The number of zero-catch trips was large in 1957 and 1958. In 1957 the estimated total number of unreported zero-catch trips was 822, or an average of about 33 per vessel; in 1958 the estimated number was 502 or about 21 per vessel. In 1959, a good year in the fishery, the estimated number of zero-catch trips for the fleet was only 128—about 6 per vessel.

The results indicate that catch per effective trip should be regarded with caution. Effective effort is a biased measure of fishing pressure, but it has been used because information on zero-catch trips was not available from the catch reports used. This condition has been remedied; in July 1964, the Hawaii Division of Fish and Game issued revised catch-report forms which have spaces for recording zero-catch trips.

DURATION OF AN EFFECTIVE TRIP

Most of the vessels in the fleet made short runs. They left for the fishing grounds in the early morning and returned to port in the evening. On occasion, however, trips of 2, 3, or 4 days have been recorded. Only a small proportion of the day was devoted to actual fishing; the greater part was spent scouting for bird flocks that follow schools of skipjack tuna.

To judge the possible effects of longer trips, the frequency of occurrence of 1- and multiple-day trips (2 or more days per trip) was determined from 1960 interview records for 16 vessels (table 5). Records for a total of 329 trips showed 315 of 1 day (95.7 percent), 13 of 2 days (4.0 percent), and 1 of 3 days (0.3 percent). Of the thirteen 2-day trips, 9 had catches during both days at sea, but each of the

TABLE 5.—*Number and percentage of 1-, 2-, and 3-day trips, total catch, catch per effective trip, and range of catches of 16 Hawaiian skipjack tuna vessels in 1960*

Days per trip	Effective trips		Catch		
			Total	Per effective trip	Range
Number	*Number*	*Percent*	*Pounds*	*Pounds*	*Pounds*
1	315	95.7	1,636,185	5,194	375–39,553
2	13	4.0	121,462	9,343	2,000–17,000
3	1	.3	35,000	35,000	----------
Totals	329	----------	1,792,647	----------	----------

remaining 4 had only 1 day in which skipjack tuna were caught. We may conclude that a trip usually represents 1 day's fishing.

AVERAGE NUMBER OF MEN HOOKING PER EFFECTIVE TRIP

The number of hooks fishing on a Hawaiian skipjack tuna vessel depends on the number of fishermen that take fishing positions along the stern during the fishing operation, since each man fishes a single pole to which a line and feathered jig is attached. Yuen (1959), in a study of the response of skipjack tuna to live bait, pointed out that the number of men hooking was one of the factors that affect the catch per school. The catch per effective trip is also related to the number of men hooking; it is important, therefore, to examine the year-to-year variation in this number. Data on the number of men hooking were available only from records collected between 1950 and 1960; those for 1950–56 and 1960 were from interview records and those for 1957–59 were from logbooks. These data were used to calculate monthly and annual averages by size classes of vessels (table 6).

Table 6.—*The monthly and annual average of the number of men hooking per effective trip on Class 1 and Class 2 Hawaiian skipjack tuna vessels, 1950–60*

Month and class		1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960
Jan.	1..	-----	-----	-----	-----	-----	-----	6.0	6.0	7.1	-----	7.0
	2..	-----	-----	-----	-----	-----	11.0	8.3	7.2	7.2	-----	7.9
Feb.	1..	-----	-----	-----	-----	-----	8.0	6.0	5.7	6.7	-----	8.2
	2..	-----	-----	-----	-----	-----	-----	8.3	6.3	6.8	-----	7.9
Mar.	1..	-----	-----	-----	8.8	9.9	9.3	-----	6.8	6.9	-----	7.1
	2..	-----	-----	-----	9.6	10.0	10.3	10.0	6.6	7.3	-----	7.4
Apr.	1..	-----	-----	-----	9.5	9.3	9.2	7.3	6.5	7.1	7.4	6.7
	2..	-----	-----	-----	9.3	9.7	9.6	10.0	7.2	7.7	7.1	7.0
May	1..	8.4	8.2	9.3	9.3	9.4	9.2	7.2	6.7	6.0	6.8	6.6
	2..	10.6	10.0	9.0	9.4	10.5	9.7	-----	8.1	8.2	8.0	7.0
June	1..	8.8	8.0	8.0	8.8	9.2	9.3	7.1	6.7	7.1	8.6	7.4
	2..	10.2	10.7	9.7	9.4	9.7	-----	-----	8.2	8.7	7.8	7.3
July	1..	8.8	7.9	8.2	8.0	8.5	8.8	7.7	7.0	8.9	8.9	6.8
	2..	9.7	8.5	9.7	9.8	9.5	9.2	-----	8.2	8.7	7.3	7.7
Aug.	1..	8.6	8.7	8.5	8.6	8.4	8.2	-----	6.3	7.9	8.4	6.5
	2..	10.8	9.7	9.1	10.3	10.1	8.3	-----	7.4	8.5	7.2	7.6
Sept.	1..	7.4	8.8	9.1	6.5	9.5	7.5	-----	5.5	5.7	7.5	6.5
	2..	10.7	9.1	9.1	10.2	9.4	7.4	-----	7.8	7.8	6.9	6.8
Oct.	1..	-----	6.2	7.8	7.9	8.5	8.0	-----	7.2	6.1	6.9	7.3
	2..	-----	8.7	8.6	-----	9.4	7.0	-----	6.7	8.0	6.6	6.7
Nov.	1..	-----	-----	8.7	9.9	10.0	8.0	-----	7.3	6.4	6.2	5.0
	2..	-----	7.0	7.0	9.9	11.9	6.0	-----	6.5	8.3	6.9	5.0
Dec.	1..	-----	-----	-----	-----	-----	-----	-----	8.0	6.6	7.0	6.5
	2..	-----	-----	-----	9.3	11.0	6.1	-----	6.8	7.9	6.7	6.4
Annual average	1..	8.4	8.2	8.4	8.6	9.2	8.9	7.1	6.7	7.1	7.6	6.9
	2..	10.4	9.6	9.2	9.7	9.8	8.3	8.7	7.4	8.1	7.2	7.4

I expected that the number of men hooking per effective trip would be greater during the season months (May to September) than during the off-season months (Shippen, 1961). Despite the incompleteness of the data for some years, the trend of change, discernible from the data for those years where information was adequate, indicates no pronounced increase in the number of men hooking in May to September (fig. 3). More men fished per effective trip in Class 2 than in Class 1 vessels, although the 1959–60 data indicate that the differences between the two classes were small.

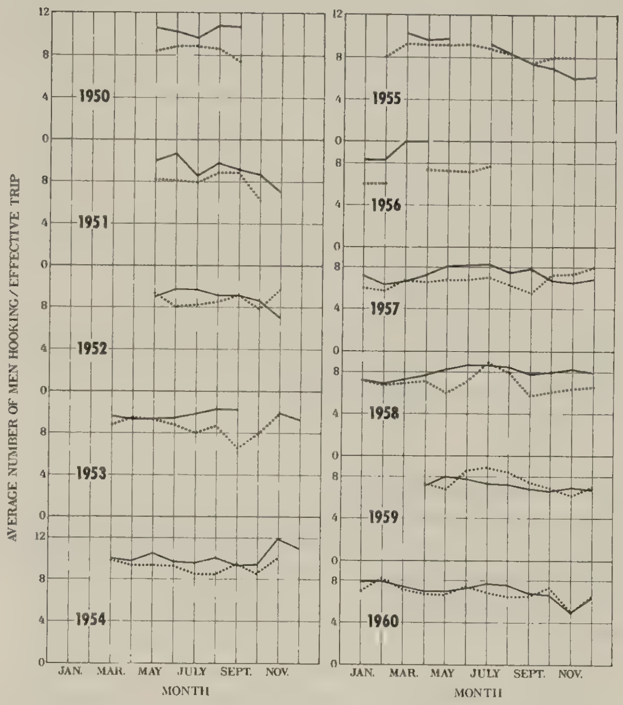

Figure 3.—Monthly averages of number of men hooking per effective trip on Class 1 and Class 2 Hawaiian skipjack tuna vessels, 1950–60. Class 1 vessels, broken line; Class 2 vessels, solid line.

Figure 4 illustrates the decline in the annual average. The average number of men hooking per effective trip on Class 1 vessels was fairly steady from 1950 to 1955, then dropped and remained at a lower level in 1956–60. The average for Class 2 vessels declined almost steadily from 1950 to 1960. This decrease in the number of men hooking from 1950 to 1960 was not, however, accompanied by a decline in the catch per effective trip. An explanation is given in the section on Apparent Abundance.

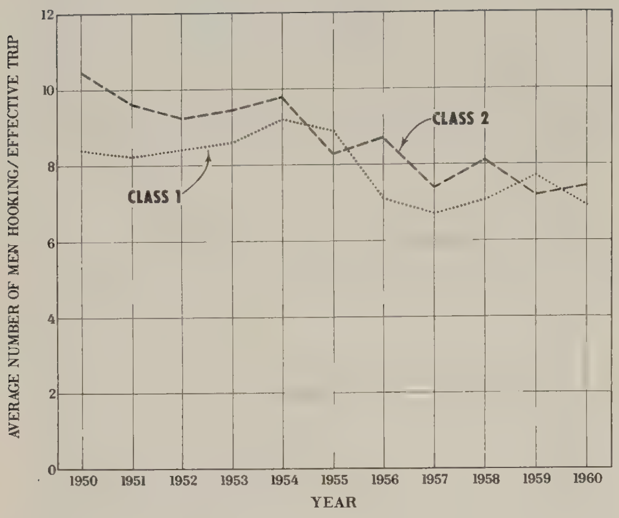

FIGURE 4.— Annual averages of number of men hooking per effective trip on Class 1 and Class 2 Hawaiian skipjack tuna vessels, 1950–60.

DISTRIBUTION OF EFFORT BY AREA

About 80 percent of the effective trips during any given year were in the inshore area (table 7). The percentage of effective inshore trips for both classes of vessels declined from 1952 to 1953. Class 1 vessels showed a further decline in 1954, then a gradual increase, whereas Class 2 vessels showed a gradual increase after 1953 (fig. 5). The percentage of effective inshore trips did not differ greatly between Class 1 and Class 2 vessels. For Class 1 vessels, the percentage of inshore trips, on the average, was 81 percent, whereas for Class 2 vessels, the average was 83 percent over the 11 years.

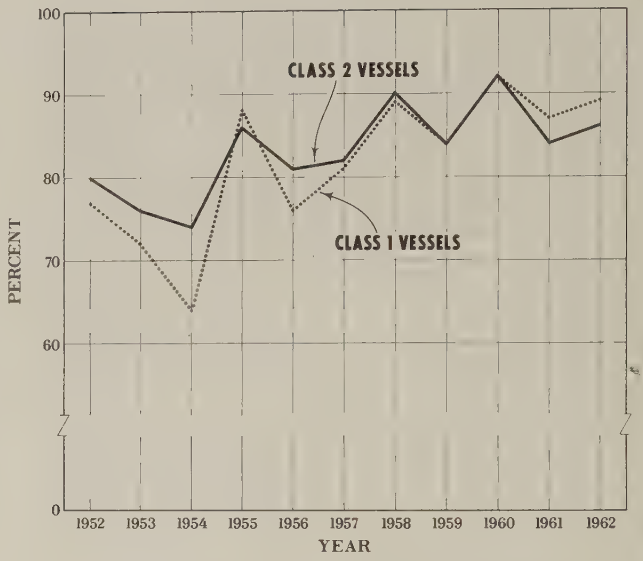

FIGURE 5.—Percentage of effective trips inshore by Class 1 and Class 2 Hawaiian skipjack tuna vessels, 1952–62.

TABLE 7.—*The number and (in parentheses) percentage of effective trips by Class 1 and Class 2 Hawaiian skipjack tuna vessels in inshore and offshore areas, 1952–62*

Year	Effective trips							
	Class 1 vessels				Class 2 vessels			
	Inshore		Offshore		Inshore		Offshore	
	Number	*Percent*	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*
1952	658	(77)	197	(23)	555	(80)	137	(20)
1953	799	(72)	308	(28)	738	(76)	232	(24)
1954	696	(70)	291	(30)	690	(77)	209	(23)
1955	817	(88)	116	(12)	748	(86)	124	(14)
1956	709	(76)	222	(24)	772	(81)	184	(19)
1957	540	(81)	128	(19)	742	(82)	168	(18)
1958	587	(89)	72	(11)	783	(90)	82	(10)
1959	658	(84)	121	(16)	884	(84)	171	(16)
1960	563	(92)	51	(8)	858	(92)	73	(8)
1961	608	(87)	88	(13)	939	(84)	179	(16)
1962	646	(89)	80	(11)	804	(86)	131	(14)
Average [1]	662	(81)	152	(19)	774	(83)	154	(17)

[1] Percentages were computed from the average annual numbers of effective trips.

A summary of effective trips by areas for each size class of vessels with respect to poor years and average and good years showed that in poor years, the percentage of effective inshore trips by Class 1 vessels was 84 percent; in average and good years, it was 81 percent. For Class 2 vessels, the values were 86 percent in poor years and 82 percent in average and good years.

One may wonder if skipjack tuna are more abundant inshore, since a larger percentage of the total trips is made within 20 miles from land. Observations of skipjack schools in Hawaiian waters in 1953 indicated that sightings of tuna schools were equally numerous offshore and inshore except for sectors to the northeast and southwest of Oahu (Royce and Otsu, 1955).

If schools are equally abundant offshore and inshore, the question arises as to why effort has been concentrated in the inshore grounds. There are several possible answers. Fishermen reduce costs by remaining close to port as long as they can make profitable catches. The concentration of effort inshore also may be dictated by the quality and quantity of live bait. Even though it may occasionally survive as long as a week, the delicate nehu may die within a few hours. The fishermen logically would fish inshore to use the bait quickly before mortality becomes heavy. Furthermore, the need to replenish live-bait supplies to some extent restricts trips to the distant offshore grounds, where live bait is unavailable.

EFFECTIVE TRIPS BY SIZE CLASSES OF VESSELS

The average number of effective trips per vessel per year fluctuated widely in 1952–62 (table 8). The average number of effective trips per Class 1 vessel per year (fig. 6) fluctuated between 51 and 72 in 1952–58, rose sharply to 97 in 1959, and ranged between 77 and 91 in 1960–62. For Class 2 vessels, the average rose very sharply from 58 to 88 in 1952–53, then declined to 75 in 1954 and to 62 in 1955. After 1955 the average appeared to increase gradually. The reason for the increase in the number of effective trips, particularly the sharp increase since 1959 among Class 1 vessels, is not known.

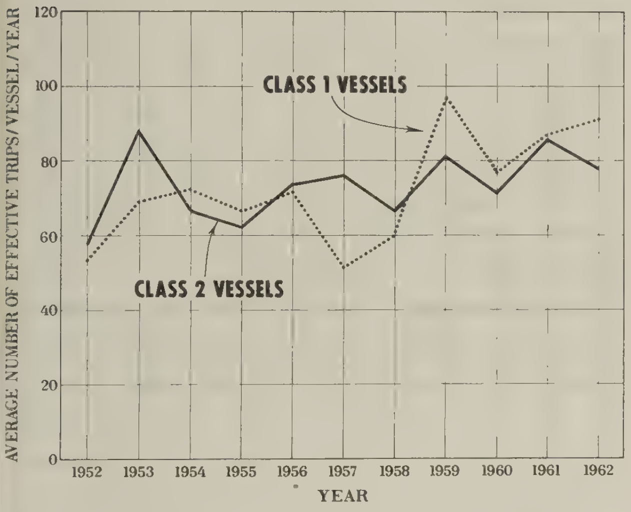

FIGURE 6.—Average number of effective trips per vessel per year by Class 1 and Class 2 Hawaiian skipjack tuna vessels, 1952–62.

TABLE 8.—*The total number of effective trips and the average number of effective trips per vessel by Class 1 and Class 2 Hawaiian skipjack tuna vessels, 1952–62*

Year	lass 1 vessels			Class 2 vessels		
	Vessels fished	Total	Average per vessel	Vessels fished	Total	Average per vessel
	Number	*Number*	*Number*	*Number*	*Number*	*Number*
1952	16	855	53	12	692	58
1953	16	1,107	69	11	970	88
1954	15	987	66	12	899	75
1955	14	933	67	14	872	62
1956	13	931	72	13	956	74
1957	13	668	51	12	910	76
1958	11	659	60	13	865	66
1959	8	779	97	13	1,055	81
1960	8	614	77	13	931	72
1961	8	696	87	13	1,118	86
1962	8	726	91	12	935	78

APPARENT ABUNDANCE

The catch per unit of effort does not provide estimates of true abundance but of apparent abundance, since it is affected by availability[1] and vulnerability[2] to the fishing gear. In the section that follows, I discuss the catch per effective trip, the factors affecting it, and the method used to obtain a standard unit of effort.

CATCH PER EFFECTIVE TRIP BY SIZE CLASSES OF VESSELS AND AREAS

Data on Y/g (catch per effective trip) by size classes of vessels and areas are given in table 9 and plotted in figure 7. The inshore Y/g for Class 1 vessels fluctuated within a relatively narrow range, whereas that for offshore fishing fluctuated more widely. The curves for Class 1 vessels offshore and Class 2 vessels inshore were similar. Catches of Class 1 vessels that fished offshore fluctuated widely and followed the curve for the total catch. The inshore and offshore Y/g for Class 1 vessels and total catch were significantly correlated ($r = 0.675$; $df = 9$; $p = 0.03$ and $r = 0.923$; $df = 9$; $p < 0.001$, respectively). A similar comparison of data for Class 2 vessels showed that both the inshore and offshore Y/g were sig-

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[1] "Availability is the portion (a percentage) of the recruited population that is physically within the geographic range of the fishery during the fishing season." (Ahlstrom, 1960: p. 1361.)

[2] "Vulnerability is the accessibility of the fish within the geographic range of the fishery to the efforts of a fishery." (Ahlstrom, 1960: p. 1361.)

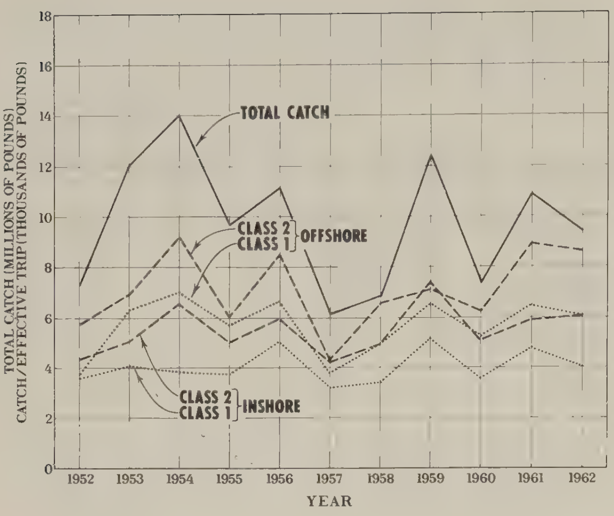

FIGURE 7.—Total catch and catch per effective trip by areas for Class 1 and Class 2 Hawaiian skipjack tuna vessels, 1952–62.

nificantly correlated with the total catch ($r = 0.762$; $df = 9$; $p<0.01$, and $r = 0.697$; $df = 9$; $p = 0.02$, respectively).

FACTORS AFFECTING ESTIMATES OF THE CATCH PER EFFECTIVE TRIP

Proper interpretation of statistics on catch and effort requires information about factors that contribute to variations in catch per unit of effort. For the skipjack tuna fishery in Hawaii, a number of factors have been isolated as causes of variation in catch per effective trip. Some of these are discussed here.

Changes in the Availability of Skipjack Tuna

In a study on the oceanography and skipjack fishery in the Hawaiian region, Seckel and Waldron (1960) pointed out that the time of initial warming of the surface water at Koko Head, Oahu, appears to be related to the annual skipjack landings. When the initial warming occurred in February, this implied that the California Current System was well developed and average or better-than-average fishing years occurred. When the initial warming occurred in March, fishing was poor.

The relation between the time of initial warming and skipjack landings later in the season appeared to have some predictive value concerning the availability of skipjack tuna. According to Seckel (1963: fig. 4), the initial warming occurred in March in 1952, 1955, 1957, 1958, and 1960; skipjack availability should be low during these years. As was pointed out earlier, however, the catch in 1955 was close to the average catch of 9.7 million pounds for 1952–62 (table 1) and was considered an average year for the purpose of this report. The forecasts made from 1959 to 1962 were dependable, but the prediction of favorable fishing conditions and catch levels could not be made with assurance because only partial understanding of the relation has been achieved. At present, variations in skipjack availability appear to be one of the most important factors causing fluctuations in the total catch of skipjack in the Hawaiian fishery.

Changes in the Number of Men Hooking and in Fishing Technique

Since the average number of men hooking per effective trip declined between 1950 and 1960, I examined the data to see if the Y/g showed a similar decline. The results (table 9 and fig. 7) showed that Y/g did not decline during 1952–62. For example, if the poor years of 1952, 1957, 1958, and 1960 are omitted to simplify the comparison, Y/g for the remaining years appears to be approximately the same before and after 1955, that is, no indication exists of a decline in Y/g. An excellent 2-year comparison is provided by the data of both size classes in 1954 and 1959, in which years

TABLE 9.—*The catch per effective trip of Class 1 and Class 2 Hawaiian skipjack tuna vessels in inshore and offshore areas, 1952–62*

Year	Catch per effective trip			
	Class 1		Class 2	
	Inshore	Offshore	Inshore	Offshore
	Pounds	*Pounds*	*Pounds*	*Pounds*
1952	3,586	3,728	4,323	5,722
1953	4,055	6,337	5,069	6,943
1954	3,867	7,758	6,312	9,210
1955	3,762	5,704	5,048	6,023
1956	4,914	6,338	5,871	8,228
1957	3,219	3,790	4,210	4,333
1958	3,238	4,928	4,723	6,593
1959	5,133	6,551	7,416	7,129
1960	3,573	5,283	5,093	6,244
1961	4,775	6,490	5,891	9,909
1962	4,019	6,071	6,066	8,602

oceanographic conditions were similar. In both years the water in the Hawaiian Islands area warmed early (Seckel and Waldron, 1960); the total catch was above average; and Y/g was also large (table 9) even though the average number of men hooking per effective trip (both classes of vessels) was 9.6 in 1954 and 7.3 in 1959.

Richard S. Shomura (personal communication) has suggested that failure of this decline in Y/g to appear may have been the result of a change in the fishing techniques necessitated by a decrease in the number of skilled fishermen. In the past, when a fisherman caught a fish, he grasped it under his arm so that he could remove the barbless hook; he then dropped the fish on the deck. (Among local fishermen, the method is called "catch" or its Japanese equivalent "daku" which means to hold in one's arm.) A considerable amount of practice and experience is required before one develops the skill necessary to fish by this method. Another method used only occasionally in the past was "flipping," in which the fisherman swings the fish aboard and suddenly relaxes the tension of the pole to permit the hook to fall clear of the fish's mouth before it drops on the deck. (This method is sometimes called "mochikomu" which in Japanese means to bring in.) Interviews with fishermen indicated that flipping allows them to catch fish faster and does not require the same degree of skill as "catching fish under the arm," but the fishermen tire more rapidly. The shift in emphasis from catching under the arm to flipping permitted a short-handed crew of limited experience to equal or better the catch of a larger and more experienced group of fishermen. Because flipping bruises the fish, some fishermen still catch under the arm when fishing large skipjack, which bring a premium price on the fresh-fish market. Damaged fish bring lower prices.

Changes in the Efficiency of Class 1 Vessels

Fishing efficiency per vessel also increases when vessels that do poorly in the fishery are forced to stop fishing. In 1952–62, the number of Class 1 vessels actively fishing decreased from 16 to 8 (2 were wrecked and 6 stopped fishing). When Class 1 vessels were ranked according to the total catch of each vessel, the results showed that the eight vessels fishing in 1962 were usually among those that were ranked high in previous years. Because those that did poorly stopped fishing, the fishing efficiency (as measured by the average catch per effective trip) of all the remaining vessels increased. This increase in fishing efficiency also may have offset the effect of the decline in the number of men hooking per trip.

The number of Class 2 vessels reached a maximum of 14 in 1955 and declined to 12 in 1962 (1 was wrecked and 1 stopped fishing). Since only one vessel in this size class has stopped fishing, the efficiency of the class could not be expected to change markedly.

Amount of Bait Used per Effective Trip

Bait supply as well as the number of men hooking per effective trip may affect catch. It is important, then, to determine whether the larger vessels do carry and use more bait than the smaller ones. Data on bait catch (table 10) permitted investigation of this problem.

TABLE 10.—*Total buckets of bait used and amount used per effective trip by Class 1 and Class 2 Hawaiian skipjack tuna vessels, 1952–62*

Year	Class 1			Class 1		
	Total buckets of bait used	Effective trips	Buckets used per effective trip	Total buckets of bait used	Effective trips	Buckets used per effective trip
	Number	*Number*	*Number*	*Number*	*Number*	*Number*
1952	12,202	855	14.3	11,319	692	16.4
1953	12,932	1,107	11.7	14,163	970	14.6
1954	12,592	987	12.8	15,503	899	17.2
1955	13,144	933	14.1	16,092	872	18.4
1956	12,092	931	13.0	14,588	956	15.2
1957	8,187	668	12.2	13,497	910	14.8
1958	5,721	659	8.7	10,966	865	12.7
1959	10,233	779	13.1	17,961	1,055	17.0
1960	5,748	614	9.4	10,593	931	11.4
1961	9,462	696	13.6	18,051	1,118	16.1
1962	9,315	726	12.8	14,733	935	15.8
Average	10,148	814	12.3	14,315	928	15.4

Class 2 vessels used more bait per effective trip in all years for which there were records. The 11-year unweighted averages indicated that Class 1 vessels used 12.3 buckets per effective trip compared with 15.4 buckets per effective trip by Class 2 vessels. The difference in the average number of buckets of bait used per effective trip between class 1 and Class 2 vessels was statistically significant

($t = -11.31$; $df = 10$; $p < 0.001$). We can conclude, therefore, that the amount of bait used in fishing contributed to the larger catch per effective trip among Class 2 vessels.

STANDARDIZATION OF CATCH PER EFFECTIVE TRIP

Differences between the large and the small vessels in numbers of men and in quantity of bait and hence in catching ability can complicate the estimation of apparent abundance. Rather than analyze data for the two classes of vessels separately, I have employed only one index, based on a "standard" unit of fishing effort. This unit is derived from a set of conversion factors which translate unequal fishing practices and capacities into a standard unit. For example, under conditions of equal abundance, when a small vessel makes a smaller catch than a large vessel, standardization of the effort units takes into account the differences in their fishing power. A general discussion of the problems in standardizing fishing effort may be found in Gulland (1955, 1956), in Shimada and Schaefer (1956), and in Schaefer (1963).

Efficiency Factors

The yearly Y/g of the two classes of vessels by areas permits the calculation of efficiency factors (Shimada and Schaefer, 1956). For each area the ratio of the yearly Y/g of Class 1 to that of Class 2 was computed. For example, from table 9, values of Y/g for 1952 were as follows:

Class 1: Inshore —3,586 pounds/effective trip
Offshore—3,728 pounds/effective trip
Class 2: Inshore —4,323 pounds/effective trip
Offshore—5,722 pounds/effective trip

For Class 1 vessels, the efficiency factor for inshore was 3,586/4,323 = 0.83; for offshore, it was 3,728/5,722 = 0.65. The efficiency factors for Class 2 vessels are fixed at 1.00 for all years. The mean efficiency factor for the year is the geometric mean of the inshore and offshore values. The geometric mean is appropriate for averaging ratios.

The mean efficiency factors for Class 1 vessels and the average for the 11-year period not only demonstrate the greater capability of Class 2 vessels, but also the variability of the factor (table 11). For example, if the Y/g of Class 1 vessels were some constant proportion of that for Class 2 vessels, one would expect an almost constant efficiency factor. The efficiency factors of Class 1 vessels, however, were as high as 0.86 and as low as 0.68. These values show no trend, and apparently are not related to good and poor years.

TABLE 11.—*Values of efficiency factors for Class 1 Hawaiian skipjack tuna vessels in terms of a fixed value of 1.00 for Class 2 vessels*

[These factors were used to standardize the unit of effort in 1952–62]

Year	Class 1	Year	Class 1
1952	0.74	1958	0.72
1953	.86	1959	.80
1954	.72	1960	.77
1955	.84	1961	.73
1956	.80	1962	.68
1957	.82	Average	.77

The efficiency factors by area (computed in terms of a fixed value of 1.00 for Class 2 vessels, offshore) for each vessel class (table 12) show that the values for both Class 1 and Class 2 were almost consistently smaller for inshore than for offshore fishing. The average for the 11-year period indicates that the offshore values of efficiency factors are higher than their respective inshore values. Furthermore, the mean efficiency factor for Class 1 offshore is slightly larger than that for Class 2 inshore. This result was not unexpected because efficiency factors do not take into account the ability of a vessel to visit distant areas where fish density may be higher. Al-

TABLE 12.—*Values of efficiency factors for Class 1 Hawaiian skipjack tuna vessels inshore and offshore and for Class 2 vessels inshore in terms of a fixed value of 1.00 for Class 2 vessels offshore*

Year	Class 1		Class 2
	Inshore	Offshore	Inshore
1952	0.63	0.65	0.76
1953	.58	.91	.73
1954	.42	.84	.68
1955	.62	.95	.84
1956	.60	.77	.71
1957	.74	.87	.97
1958	.49	.75	.72
1959	.72	.92	1.04
1960	.57	.85	.82
1961	.48	.65	.59
1962	.47	.70	.70
Average	.57	.80	.78

though it may appear from the values of efficiency factors in table 11 that Class 2 vessels always have better results than Class 1 vessels, the data indicate that, on the average, the offshore catches of Class 1 vessels are likely to be larger than those of Class 2 vessels fishing in inshore waters.

Catch per Standard Effective Trip

The efficiency factors, given in table 11, were used in calculating the standard unit of effort. For example, in 1952 there were 855 effective trips by Class 1 vessels and 692 by Class 2 vessels. The standard effective trip is the sum of the products of the mean efficiency factor and total number of effective trips of the size classes:

$$0.74(855) + 1.00(692) = 1{,}325$$ standard effective trips. The catch per standard effective trip (Y/f; the notation f refers to fishing effort expressed in standard effective trips) is found by dividing the sample catch by the standard effective trips:

$$\frac{6{,}277{,}046}{1{,}325} = 4{,}737 \text{ pounds per standard effective trip;}$$

and the fishing intensity is obtained from the total catch and Y/f:

$$\frac{7{,}291{,}851}{4{,}737} = 1{,}539 \text{ standard effective trips.}$$

The Y/f reflects only apparent abundance based on the trips on which fish were caught. The total catch of skipjack tuna in pounds, Y/f, and relative effective fishing intensity per Class 2 trip are presented in table 13 and the index curves are illustrated in figure 8.

Table 13.—*Total landings of skipjack tuna in Hawaii, catch per standard effective trip, and relative effective fishing intensity, 1952–62*

Year	Total catch	Catch per standard effective trip (Class 2 trip)	Relative effectivefishing intensity (in Class 2 trips)
	Thousand pounds	*Pounds*	*Trips*
1952	7,292	4,737	1,539
1953	12,059	5,486	2,198
1954	14,021	6,983	2,008
1955	9,694	4,986	1,944
1956	11,132	6,430	1,731
1957	6,130	4,166	1,471
1958	6,834	4,850	1,409
1959	12,413	7,119	1,744
1960	7,360	5,062	1,454
1961	10,894	6,629	1,643
1962	9,415	6,358	1,481

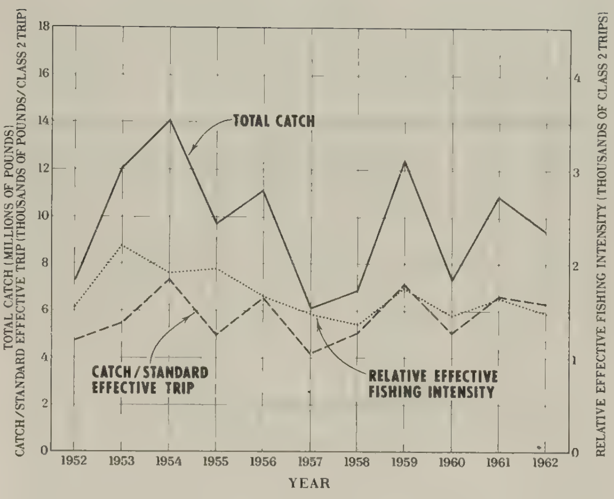

Figure 8.—Total catch, catch per standard effective trip, and the relative effective fishing intensity for skipjack tuna in Hawaii, 1952–62.

The curve for Y/f was at 4,737 pounds in 1952, rose in 1953 and again in 1954 to reach a peak of 6,983 pounds, then dropped to about the 1952 level in 1955. Another peak in 1956 was followed by a decline to its lowest level in 1957. The Y/f reached another peak in 1959, surpassing that of 1954. The Y/f had no trend; rather, the values varied around an average of about 5,700 pounds per standard or Class 2 trip. The relative effective fishing intensity exhibited a slight decreasing trend from about 1953 to 1958 and leveled off at about 1,600 standard trips in 1959–62.

INTERRELATION OF TOTAL CATCH, FISHING INTENSITY, AND APPARENT ABUNDANCE

The catch per standard effective trip (Y/f) and the total catch fluctuated in a similar fashion in 1952–62 ($r = 0.851$; $df = 9$; $p < 0.001$). For the 11-year period, then, the total catch may be used as an index of apparent abundance, but it should by no means be considered an appropriate index in other years. The situation may change in other years, because of the sensitivity of the total landings to various influences such as weather, sea conditions, the amount of effort expended, and the market for skipjack tuna.

The Y/f and the relative effective fishing intensity were not correlated significantly over the 11-year period ($r=0.343$; $df=9$; $p = 0.32$). The lack of correlation suggested that changes in the size of the Y/f were not influenced by changes in the amount of fishing, but by other fishery-independent factors, such as variation in availability and vulnerability; the strength of year classes also may be important (Rothschild, 1965). The effective fishing intensity tended to decline over the years under study, largely because of a decrease in the number of vessels in the fleet.

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CHARACTERISTICS OF THE BLOOD OF ADULT PINK SALMON AT THREE STAGES OF MATURITY

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ABSTRACT

Selected characteristics of the blood of adult pink salmon (*Oncorhynchus gorbuscha*) were studied in fish at three stages of maturity—migrating fish approaching the general area of spawning streams but still in the open ocean, fish in the immediate vicinity of the spawning stream but in the estuary, and fish in the spawning stream. Although some hematological characteristics changed little, blood proteins, glucose, and cholesterol decreased progressively, and lipid phosphorus increased.

The blood chemistry of salmon of the genus Oncorhynchus is especially interesting because of physiological changes that occur during the spawning migration from sea water to estuarine waters of reduced salinity and then into fresh water. This change in the environment is concurrent with the final stages of maturation.

Some information is already available on changes in blood characteristics at this time of the life cycle. Lysaya (1951) found several physiological changes in the blood with advancing sexual maturity in the Asiatic pink salmon (*O. gorbuscha*) and chum salmon (*O. keta*). The erythrocyte count, the hemoglobin concentration, and the blood glucose, chloride, and calcium levels fell; and the erythrocyte sedimentation rate and the blood urea and nonprotein nitrogen concentrations increased. Biologists of the Fisheries Research Board of Canada found that adult sockeye salmon (*O. nerka*) on their spawning migration up the Fraser River lost 11 to 30 percent of their body weight and had decreasing blood cholesterol (Idler and Tsuyuki, 1958); liver glycogen decreased, except for a terminal increase (Chang and Idler, 1960); and concentrations of adrenal corticosteroid hormones increased (Idler, Ronald, and Schmidt, 1959). Chinook salmon (*O. tshawytscha*) during their spawning migration up the Sacramento River and its tributaries in California showed: increased activity of the pituitary with terminal degeneration; hypertrophy of the islets of Langerhans; hyperplasia of the adrenal cortices (a rise in concentration of 17-hydroxycorticosteroids ended with degeneration of the adrenal glands); and the deterioration of the stomach, liver, spleen, thymus, kidneys, thyroid, and cardiovascular system (Robertson and Wexler, 1960, 1962; Robertson, Krupp, Favour, Hane, and Thomas, 1961; Robertson, Wexler, and Miller, 1961; and Robertson, Krupp, Thomas, Favour, Hane, and Wexler, 1961).

In 1963, under the sponsorship of the Bureau of Commercial Fisheries, I had the opportunity to study the hematology and blood chemistry of adult pink salmon in three stages of maturity in Alaska: (1) maturing fish in salt water migrating toward the spawning areas; (2) nearly mature fish milling in the estuary of a small creek; and (3) mature fish spawning in a fresh-water stream. This paper reports the results of these studies.

COLLECTION OF SAMPLES

Pink salmon in the three stages of maturity were taken from three stocks on different dates. Those migrating toward the spawning grounds (termed "migrating"), were taken from the open ocean near the community of Elfin Cove, southeastern Alaska. They were captured on August 5, about a month before

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they would have spawned; only males were sampled. Salmon milling at the mouth of a creek (called "prespawning") were taken August 9, about 2 weeks before the start of movement into fresh water, from a bay at the mouth of a stream at Little Port Walter on the southern end of Baranof Island, southeastern Alaska; equal numbers of males and females were sampled. Salmon spawning in the stream (termed "spawning") were taken from Olsen Creek, which empties into Olsen Bay on Port Gravina, Prince William Sound. They were taken on July 19 (males only) and September 2 (males and females). The Olsen Creek fish, which made up more than half of all the pink salmon sampled, were sampled on two dates because they arrive in two distinct runs. The early run typically lasts from mid-July to mid-August and the late one from late August to middle or late September. These populations may be genetically distinct.

One sample of blood was taken from each specimen while the fish was held on its back, in a wooden trough. A no. 18-½ needle on a syringe was inserted into the dorsal aorta above the roof of the pharynx, in the region of the second gill arch, and 12 ml. of blood were withdrawn. About 0.2 g. (a pinch) of potassium oxalate, an anticoagulant chosen because it is dry and hence does not cause dilution, was placed in the syringe before the sample was taken. The blood was transferred to a capped vial that also contained a pinch of the oxalate and was placed in an iced, insulated chest and transported by plane to the Bureau of Commercial Fisheries Biological Laboratory at Auke Bay. About 24 hours elapsed between collection and analysis of blood.

HEMATOLOGY

Certain hematological characteristics were determined. Specific gravity was measured by standard methods; packed cell volume was estimated after the samples were centrifuged in Wintrobe tubes at 2,700 r.p.m. for 15 minutes; erythrocytes were counted by standard techniques (Wintrobe, 1933) with 0.85 percent saline as a diluent; and hemoglobin was determined with Hycel[1] cyanomethemoglobin reagents. Mean corpuscular volume, mean corpuscular hemoglobin, and mean corpuscular hemoglobin concentration were calculated by the formulas of Wintrobe (1933). A current general reference for work of this type is that of Hesser (1960).

The results of the analyses (table 1) are discussed in comparison with the results of other workers. Because most of the characteristics did not vary among the three stages

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[1] Trade name referred to in this publication does not imply endorsement of commercial product.

TABLE 1.—*Certain hematological characteristics of adult pink salmon in three stages of maturity from three areas of Alaska in 1963*

[Numbers in parentheses are numbers of samples analyzed]

Stages of maturity	Mean specific gravity	Mean packed cell volume	Mean erythrocytes	Mean hemoglobin	Mean corpuscular volume [1]	Mean corpuscular hemoglobin [2]	Mean corpuscular hemoglobin concentration [3]
		Percent	*Number/mm.³×10⁶*	*Grams/100 ml.*	μ^3	*Micro micrograms*	*Percent*
Migrating (Elfin Cove)							
Males	1.061(16)	42(15)	0.98(15)	11.3(15)	439(15)	118(15)	27(15)
Prespawning (Little Port Walter)							
Males and females	1.057(15)	38(15)	.97(15)	10.7(15)	396(15)	114(15)	28(15)
Spawning (Olsen Creek)							
Males	1.059(31)	38(29)	1.01(29)	11.1(29)	403(29)	117(29)	30(29)
Females	1.058(8)	32(8)	.94(8)	10.5(8)	354(8)	114(8)	32(8)
Combined [4]							
Mean	1.059(62)	39(59)	.97(59)	11.0(59)	410(59)	116(59)	28(59)
Standard deviation	.004	4.5	.17	.9	69	22	3
Range	1.050–1.065	32–52	0.53–1.35	8.7–13	270–641	84–196	21–38

[1] $\text{MCV} = \frac{\text{Volume of red blood cells in 1,000 ml. blood}}{\text{Red blood cell count in million/mm.}^3}$

[2] $\text{MCH} = \frac{\text{Hemoglobin in grams per 1,000 ml. blood}}{\text{Red blood cell count in million/mm.}^3}$

[3] $\text{MCHC} = \frac{\text{Hemoglobin in grams percent} \times 100}{\text{Packed cell volume}}$

[4] Female pink salmon from Olsen Bay not included.

of maturity, only the mean from each stage and the grand average, range, and standard deviation for the three stages combined are given in table 1. Statistical comparisons were made by the one-way analysis of variance, or F-test (Li, 1957). No distinction is made here between early- and late-run salmon at Olsen Creek.

The specific gravities, erythrocyte counts, and hemoglobin concentrations fall within the ranges of those listed by Wintrobe (1933) for oceanic bony fishes, although the mean corpuscular volume and mean corpuscular hemoglobin were high and are comparable with the more primitive fishes.

In the comparison of my present findings on hematology of pink salmon with those of other workers, several points are of interest. In California, Robertson, Krupp, Favour, Hane, and Thomas (1961) found for chinook salmon that erythrocyte counts, hemoglobin levels, and packed-cell volumes increased during the migration and decreased during the spawning stage (to levels similar to those in animals in the open sea). My findings agree with those of Robertson and his associates in that packed-cell volumes (fig. 1) were higher in migrating males than in spawning males. The packed-cell volumes in combined male and female samples were also higher in prespawning populations than in spawning populations. Within the spawning population, the males had greater packed-cell volumes than the females. A significant increase (at the 2.5-percent level) in mean corpuscular hemoglobin concentration between the prespawning and the spawning stages was concurrent with the small decrease in packed-cell volume.

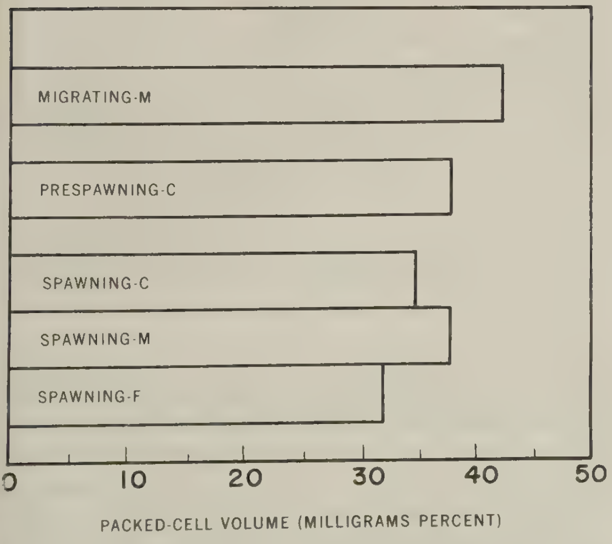

FIGURE 1.—Packed-cell volume of blood of adult pink salmon in three stages of maturity. (C, sexes combined; F, females; M, males.)

In his studies of pink salmon in Asia, Lysaya (1951) found that erythrocyte counts and hemoglobin levels fell noticeably between the time fish entered the estuary and the time they arrived on the spawning grounds. Such a trend is clearly evidenced by the decrease in packed-cell volume in my study, although it is not noticeable in the erythrocyte and hemoglobin values. The absence of a difference in hemoglobin concentrations between prespawning and spawning stages in my work, was also reported by Sinderman and Mairs (1961) for the alewife, *Alosa pseudoharengus*, a fish that returns to the sea after spawning in fresh water.

Benditt, Morrison, and Irving (1941) found that in Atlantic salmon (*Salmo salar*) affinity of hemoglobin for oxygen was greater while fish were in the spawning stage in fresh water than in the prespawning or migrating stage in salt water. This last phenomenon would compensate those changes mentioned above that would tend to decrease the oxygen-carrying efficiency of the blood. Perhaps an understanding of these points will be possible when larger numbers of fish are analyzed at all stages of migration.

BLOOD CHEMISTRY

The concentrations of several components of blood (table 2) were determined by the techniques given in Fister (1950). As with the hematology and corpuscular indices, the measured values of some of the characteristics of blood did not vary significantly among the three stages of maturity; only the mean from each stage and the mean, range, and standard deviation for the three stages combined are given in table 2.

TABLE 2.—*Average values in blood chemistry of adult pink salmon at three stages of maturity from three areas of Alaska in 1963*

[Numbers in parentheses are numbers of samples analyzed]

Stage of maturity	Albumin [1]	Globulin [1]	Glucose [2]	Cholesterol [1]	Lipid phosphorus [2]	Uric acid [2]	Urea [2]	Creatinine [2]
	Grams percent	*Grams percent*	*Milligrams percent*	*Milligrams percent*	*Milligrams percent*	*Milligrams percent*	*Milligrams percent*	*Milligrams percent*
Migrating (Elfin Cove)								
Males	1.5(11)	0.4(12)	101(16)	835(10)	----------	2.2(16)	4.1(15)	1.0(16)
Prespawning (Little Port Walter)								
Males	1.3(8)	.7(8)	----------	----------	----------	1.4(8)	5.1(15)	----------
Females	.7(8)	1.0(8)	----------	----------	----------	2.1(8)	----------	----------
Combined	----------	----------	68(16)	656(14)	5.8(14)	----------	----------	----------
Spawning (Olsen Creek)								
Males	1.8(26)	.6(23)	----------	----------	----------	----------	7.4(23)	1.2(16)
Early run	----------	----------	78(16)	494(16)	15.9(14)	.7(16)	----------	----------
Late run	----------	----------	43(11)	580(14)	11.3(16)	1.5(16)	----------	----------
Females								
Late run	.6(5)	.4(5)	41(8)	542(7)	17.5(8)	1.7(5)	6.7(6)	----------
Combined [3]								
Mean	1.5(53)	.7(51)	75(59)	621(54)	11.0(44)	1.6(64)	5.8(53)	1.1(32)
Standard deviation	.6	.4	30	136	3.3	.5	5.2	.5
Range	.5-3.4	.2-1.2	23-167	364-1,220	2.5-20.5	.3-2.9	.5-28	.3-2.9

[1] Plasma.

[2] Whole blood.

[3] Female pink salmon from Olsen Bay not included in combined values.

ALBUMIN AND GLOBULIN

Albumin and globulin are discussed together because both are blood proteins. Comparisons are made between males and females (table 2) in the three spawning stages (figs. 2 and 3).

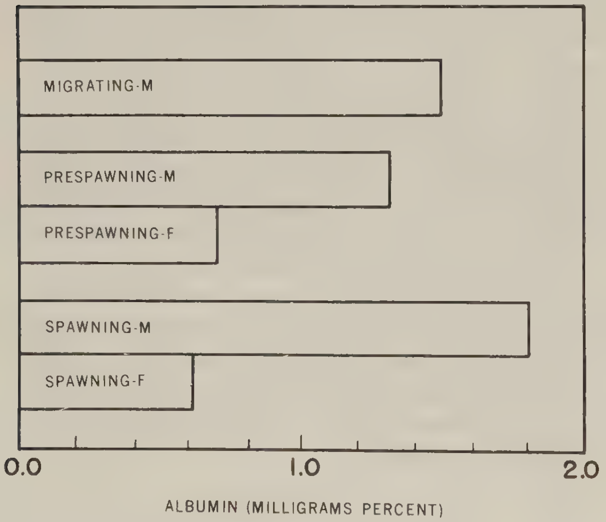

FIGURE 2.—Albumin of blood of adult pink salmon in three stages of maturity. (F, females; M, males.)

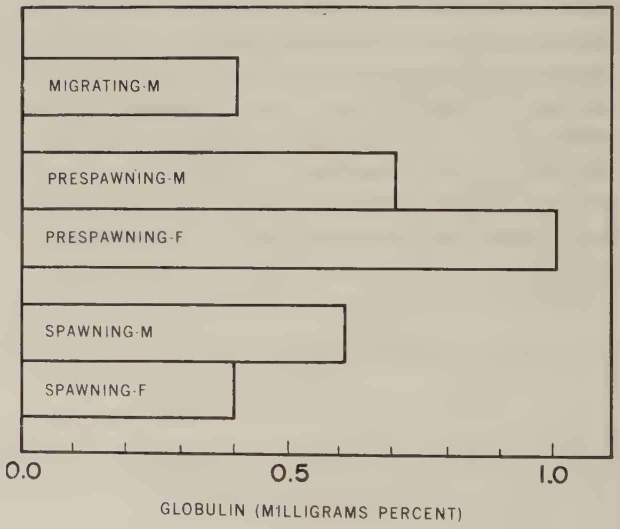

FIGURE 3.—Globulin of blood of adult pink salmon in three stages of maturity. (F, females; M, males.)

Although the range in values was large, the average concentrations of components in males showed little change from the migrating through the prespawning and spawning stages. The albumin-globulin ratio was greater than 1:1—the ratio considered normal for mammals and most fishes (Shell, 1961). The albumin values for prespawning females were about half of those for prespawning males, whereas the globulin values for prespawning females averaged higher than those for males (table 2). The albumin–globulin ratio was 0.7:1 for prespawning females. The globulin was greatly reduced in spawning females, and the albumin-globulin ratio (1.5:1) was more nearly like the ratio for spawning males (3:1). The results of my analysis of albumin and globulin are consistent with those of Robertson, Krupp, Favour, Hane, and Thomas (1961), who found that the normal ratio of albumin to globulin of 1:2 in chinook salmon living in the sea was reversed in both sexes during migration but tended to revert to the original during spawning.

The greater reduction of albumin and globulin in females than in males by spawning time probably indicates a greater depletion of body protein in egg formation. Shell (1961), who surveyed the nutritive, osmotic, and other functions of blood proteins in fish, found a cyclic reversal of the albumin-globulin ratio in smallmouth bass, *Micropterus dolomieui,* and in his review of the literature stated that "Results of determinations of the A:G ratio in fish are confusing."

GLUCOSE

My discussion of glucose levels includes comparisons between pink salmon in the migrating and the prespawning stages and between pink salmon in early and late runs (fig. 4 and table 2). The drop in glucose between the migrating and prespawning fish is significant at the 1-percent level, and the decrease from early to late spawners is significant at the 2.5-percent level. The different levels of glucose in spawning salmon may be attributed to the fact that the salmon of the early run at Olsen Creek were not completely ready to spawn, whereas the fish of the late run were actually spawning. The findings are in accord with those of Lysaya (1951).

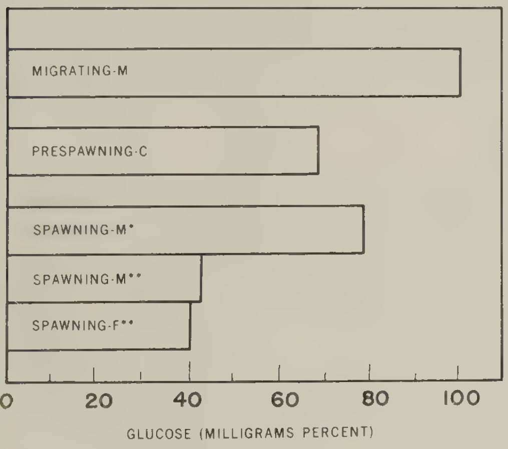

FIGURE 4.—Glucose of blood of adult pink salmon in three stages of maturity. (C, sexes combined; F, females; M, males; single asterisk, early run; double asterisk, late run.)

It is commonly assumed that carbohydrate metabolism in fish is inefficient. Robertson and Wexler (1960), however, found an increase in the number and size of islets of Langerhans in chinook salmon during the spawning migration. Robertson, Krupp, Favour, Hane, and Thomas (1961) found an increase in blood glucose while fish were migrating from the open sea, followed by a tendency toward a decrease during spawning. They suggested that rising levels of blood glucose are due to gluconeogenesis that results from the action of increasing adrenal corticoids on muscle and fat deposits and a simultaneous increase in insulin production to utilize the product.

This viewpoint is somewhat corroborated by studies on the Fraser River in which sockeye salmon have shown an 11- to 30-percent loss of body flesh (Idler and Tsuyuki, 1958) accompanying increased production of adrenal corticosteroid hormones (Idler et al., 1959). Chang and Idler (1960) observed that liver glycogen gradually decreased during migration in fresh water but increased at spawning. These changing glycogen levels were attributed to changing hormone balances.

CHOLESTEROL

Cholesterol levels are compared among the three stages of maturity (fig 5). A downward trend in cholesterol levels from the migrating to the spawning stage was consistent, i.e. significantly lower (at the 1-percent level) in the prespawning than the migrating fish and in the spawning than the prespawning fish. Robertson, Krupp, Favour, Hane, and Thomas (1961) and Idler and Tsuyuki (1958) observed this same consistent downward trend in chinook salmon. Although I found this downward trend in cholesterol levels from the migrating to the spawning stage, levels in pink salmon within the spawning group were higher in the late run than in the early run.

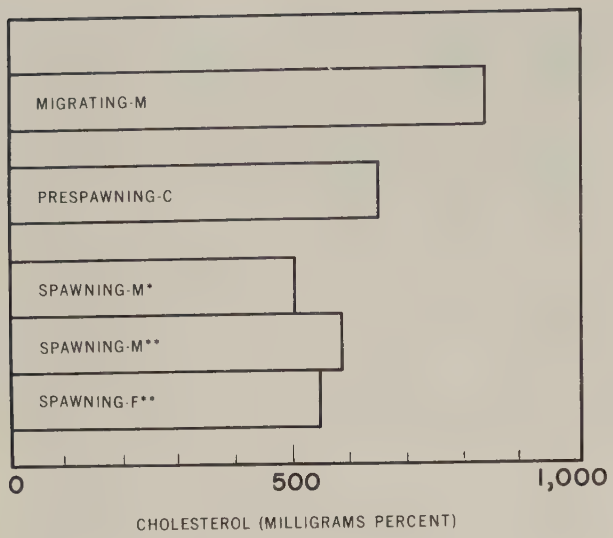

FIGURE 5.—Cholesterol of blood of adult pink salmon in three stages of maturity. (C, sexes combined; F, females; M, males; single asterisk, early run; double asterisk, late run.)

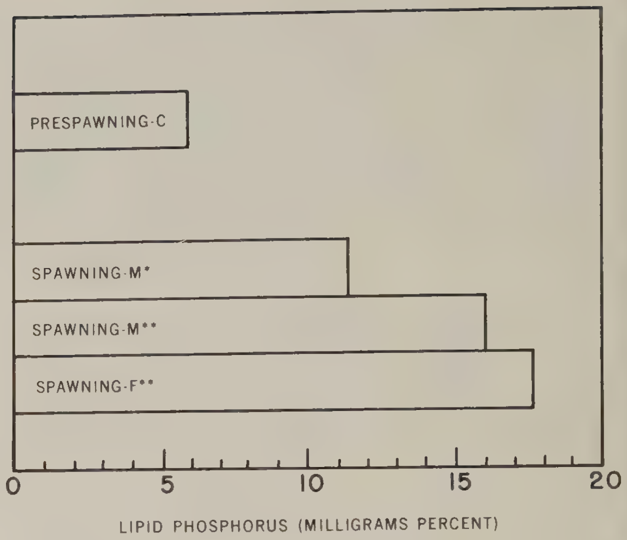

FIGURE 6.—Lipid phosphorus of blood of adult pink salmon in two stages of maturity. (C, sexes combined; F, females; M, males; single asterisk, early run; double asterisk, late run.)

The function of cholesterol in the metabolism of fishes (reviewed by Shell, 1961) remains obscure. In my study, however, cholesterol showed an inverse correlation with lipid phosphorus (significant at the 1-percent level).

LIPID PHOSPHORUS

Concentrations of lipid phosphorus in samples from the prespawning and spawning stages and the early and late spawning runs are compared (fig. 6). No data are available from the migrating group. The increase in lipid phosphorus levels from the prespawning to the spawning stage was significant at the 1-percent level. The values for males in the spawning stage in the early part of the run (fig. 6) were also significantly higher than in the late run (at the 1-percent level.) The high values for lipid phosphorus in the females sampled in the late run may be due to a terminal increase in 17-hydroxycorticosteroids in females as values at that time are dropping in males (Hane and Robertson, 1959). Although Shell (1961) found a direct correlation between lipid phosphorus and the blood proteins (albumin and globulin), no such correlation is evident in my data. Comparisons between individual animals, however, indicated a positive correlation (1-percent level of significance) with glucose. The results suggest a mechanism whereby the concentration of lipid phosphorus increases as cholesterol and glucose decrease.

URIC ACID

The values for uric acid are discussed for males and females in the three stages of maturity. The decline in uric acid concentration in the blood of males from the migrating to the prespawning stage is significant at the 1-percent level (fig. 7). The further drop in uric acid from the prespawning to the early part of the spawning stage (in the early run only) is also significant at the 1-percent level. No such drop is apparent, however, in the comparison of the males of the prespawning and the late part of the spawning stage (fig. 7). Within the prespawning stage, uric acid values were higher in the females than in the males (significant at the 5-percent level). Uric acid concentrations in females from the late spawning stage average only slightly higher than those in the males (table 2). If uric acid is accepted

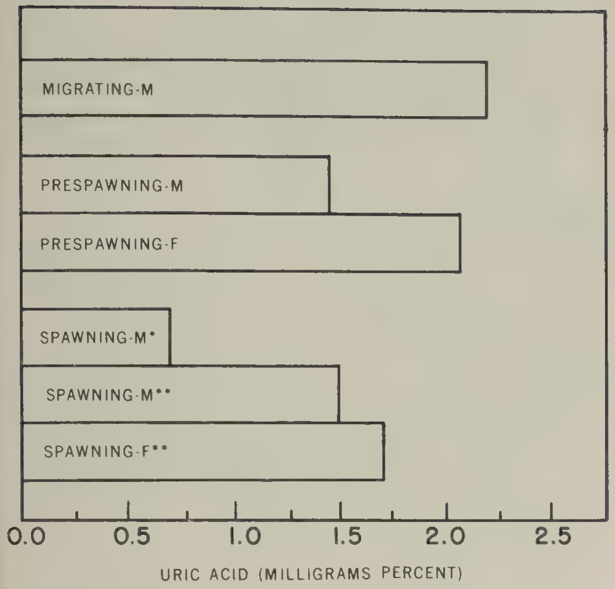

FIGURE 7.—Uric acid of blood of adult pink salmon in three stages of maturity. (F, females; M, males; single asterisk, early run; double asterisk, late run.)

as an end product of purine metabolism, a decline in purine metabolism at spawning is indicated, and females maintain a higher level longer than males.

UREA

The variations in the concentration of urea among individual specimens from an area were so great that no trend is apparent for this blood component, which is the end product of nitrogen metabolism. Lysaya (1951) noted increasing concentrations as spawning approached and attributed death of pink and chum salmon to urea poisoning.

CREATININE

No data are available on the concentrations of creatinine in blood samples from fish in the prespawning stage, and no trend is indicated by the values for the other groups. Creatinine is sometimes considered an end product of tissue catabolism, which is a dominant process in the fish sampled here. The values I found, however (table 2), are similar to those determined for smallmouth bass by Shell (1961) and for carp (*Cyprinus carpio*) and brook trout (*Salvelinus fontinalis*) by Field, Elvehjem, and Juday (1943) for fish in which catabolism was not high.

SUMMARY AND CONCLUSIONS

Blood samples were taken from adult pink salmon collected at three stages of maturation during their migration to the spawning grounds—in the ocean actively migrating, milling in the estuary of a spawning stream, and in fresh water on the spawning grounds.

Basic hematological characteristics, including specific gravity, packed-cell volume, erythrocytes, hemoglobin, corpuscular volume, corpuscular hemoglobin, and corpuscular hemoglobin concentration, were determined. Statistical analyses indicated no significant difference among groups of fish.

The concentrations of several components of blood indicate that several changes accompany migration and maturation. As pink salmon mature, utilization of protein reserves (evidenced by lowered albumin and globulin levels in females) may result from rapid building of egg tissue. Glucose levels declined, especially in females. Cholesterol concentrations also declined, although lipid phosphorus rose in both sexes; the increase was especially noticeable in females. Lipid phosphorus may play an increasingly important part in energy transfer as salmon mature.

The pink salmon from the spawning stream were from two distinct components of the run—the early and the late. The late spawners had significantly higher concentrations of cholesterol and uric acid, but lower levels of glucose and lipid phosphorus. I do not know if these differences are due to intrinsic genetic factors or are induced by extrinsic environmental factors.

I could see no trend in urea or creatinine concentrations at the three stages of maturity.

ACKNOWLEDGMENTS

David Boye and Mrs. Frances Pierce helped with the statistical comparisons. Theodore R. Merrell, Jr., and several other staff members at the Bureau of Commercial Fisheries Biological Laboratory, Auke Bay, Alaska, aided in collecting samples. This work was financed by the Bureau of Commercial Fisheries under Contract No. 14-17-0005-46 with funds made available under the Act of July 1, 1954 (68 Stat. 376) commonly known as the Saltonstall-Kennedy Act.

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CROSS-REACTIVE PROPERTIES OF ANTISERA PREPARED IN RABBITS BY STIMULATIONS WITH TELEOST VITELLINS

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ABSTRACT

Antisera were prepared by injecting rabbits with egg or serum vitellin preparations from seven teleost species belonging to different families. The ranges of reactivity of these antisera were tested with sera from mature females of nine teleost families as well as with sera from females of spiny dogfish, Pacific lamprey, and white sturgeon. All of these antisera reacted with vitellins from all species tested from the homologous families. Antisera prepared against rockfish and flounder vitellins cross-reacted with sera from mature females of all teleost species tested. A greater antigenic complexity in the vitellins of more taxonomically advanced species than more primitive species is indicated by the results of the reactions and absorption tests. The results are of practical importance in studies on maturity of fishes and have theoretical implications in the field of systematics.

Fishery researchers have used serological techniques with increasing frequency since 1950. Much of the work has been directed toward identification of populations either through blood-grouping techniques or studies of variable serum antigens (Cushing, 1964). Ridgway, Klontz, and Matsumoto (1962) observed a characteristic antigen in the serum of maturing and mature female sockeye salmon (*Oncorhynchus nerka*). A review of the literature and subsequent studies by our group has revealed that similar components occur not only in all the teleosts but also in all vertebrate classes were oviparity occurs (Urist and Schjeide, 1961; Drilhon and Fine, 1963). These antigens appear to have considerable practical value in investigations of maturity in female fish because of their connection with the process of sexual maturation (Ho and Vanstone, 1961; Olivereau and Ridgway, 1962; Ridgway, 1964; Utter and Ridgway, 1966).

The function of the blood serum as a transporting medium between the site of synthesis in the liver and the site of storage in the ovary appears to explain the presence of yolk components in the blood (Vanstone, Maw, and Common, 1955). The serum vitellins studied have displayed similar biochemical properties, are characterized as phospholipoproteins, and conform to the classical description of avian vitellin as the water-insoluble fraction of the egg yolk (Jukes and Kay, 1932; Vanstone, Maw, and Common, 1955).

This report is based on data obtained through testing numerous antisera for cross-reactive properties. The antisera were prepared in rabbits against vitellins of teleosts. We intend to bring out points of both practical significance and theoretical interest.

METHODS AND MATERIALS

IMMUNOLOGICAL TESTS

A microslide adaptation of the double diffusion method of Ouchterlony as modified by Ridgway, Klontz, and Matsumoto (1962) was used for all serological tests. The agar medium consisted of 1.5 percent Difco agar, 0.72 percent sodium chloride, 0.60 percent sodium citrate, 0.01 percent merthiolate, and 0.01 percent trypan blue. Wells were punched in the agar at 8-mm. intervals and filled to a volume of about 0.01 cc. of reactant. Slides were evaluated after 24 hours of incubation at 37° C.

PRODUCTION OF ANTISERA

Table 1 lists the antisera used in this study. Egg vitellin preparations were made by blending and centrifuging one part eggs with three

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TABLE 1.—*Antisera used in this study*

Designation	Vitellin source	Number of rabbits
Anti-CLM	Pacific herring (*Clupea harengus pallasi*) eggs	1
Anti-SM	Chinook salmon (*Oncorhynchus tshawytscha*) eggs	3
Anti-CM	Northern squawfish (*Ptychocheilus oregonensis*) eggs.	1
Anti-GM	Pacific cod (*Gadus macrocephalus*) serum	1
Anti-TM	Yellowfin tuna (*Thunnus albacares*) eggs	1
Anti-RM	Copper rockfish (*Sebastodes caurinus*) eggs	3
Anti-HM	Starry flounder (*Platichthys stellatus*) eggs	5

parts 1 percent saline in a Waring Blender.[2] After centrifugation, the addition of 11 parts of distilled water precipitated the vitellins from the supernatant fluid. The precipitate was dissolved again in saline, reprecipitated and redissolved, and used for injections. Whole serum from a mature female Pacific cod was used to produce the anticod vitellin reagent. The resulting antiserum was absorbed at a 1:1 ratio with male cod serum before testing. Usually the vitellin-bearing materials were suspended in a bayol-arlacel mixture and injected into the rabbits intraperitioneally. Consistently uniform results were obtained when other injection procedures were used, but a greater number of injections was usually required. Single bleedings were used for testing with the exception of the reagent prepared against starry flounder vitellin which was a pool of numerous bleedings from five rabbits. The antisera produced in different rabbits injected with the same vitellin material were qualitatively very similar. This uniformity of reagent indicates that the differences reported later are not due to variations in the immune response of individual rabbits.

COLLECTION OF SERUM SAMPLES

Samples of fish serum were taken from whole blood that had been processed within 48 hours after collection; the samples were then stored at -35° C., a temperature at which the vitellin fraction appeared to be stable. Some sera had been stored as long as 8 years when tested.

REACTIVE PROPERTIES OF THE ANTISERA AND VITELLINS TESTED

Table 2 summarizes the data obtained through testing of sera from mature females of various fish species. All antisera were tested with the same fish sera; this testing included males as well as females from most species. The only reaction with male serum occurred between the antirockfish reagent and male rockfish serum. This reaction was very weak and was most likely the result of nonvitellin antigens present in the injected material. The reaction with male rockfish sera could not be confused with the reaction with female rockfish sera.

TABLE 2.—*Cross-reactivity of rabbit antiteleost vitellin sera with vitellins of fish representing various taxonomic groups* [1]

[X = strong reaction; W = weak reaction; 0 = no reaction]

Reagent	Nonteleosts			Teleosts								
	Agnatha (1)	Chondrichthys (2)	Chondrostei (3)	Clupeid (4)	Salmonid (5)	Cyprinoid (6)	Gadid (7)	Scombrid (8)	Scorpaenid (9)	Cottid (10)	Pleuronectid (11)	Batrachoidid (12)
Anti-												
Clupeid (CLM)	0	0	0	X	0	0	0	0	W	0	0	0
Salmonid (SM)	0	0	0	0	X	0	0	0	W	0	0	0
Cyprinid (CM)	0	0	X	0	W	X	0	0	0	0	0	0
Gadid (GM)	0	0	0	0	0	0	X	W	0	0	0	0
Scombrid (TM)	0	0	0	W	W	W	X	X	X	X	X	0
Scorpaenid (RM)	0	0	X	X	X	X	X	X	X	X	X	X
Pleuronectid (HM)	0	0	0	X	X	X	X	X	X	X	X	X

(1) Pacific lamprey, *Lampetra tridentata;* (2) spiny dogfish, *Squalus acanthias;* (3) White sturgeon, *Acipenser transmontanus;* (4) shad, *Alosa sapidissima;* Pacific herring, *Clupea harengus pallasi;* (5) sockeye salmon, *Oncorhynchus nerka;* (6) carp, *Cyprinus carpio;* northern squawfish *Ptychocheilus oregonensis;* largescale sucker, *Catostomus macrocheilus;* (7) Pacific hake, *Merluccius productus;* Pacific cod, *Gadus macrocephalus;* (8) bigeye tuna, *Thunnus obesus;* Pacific mackerel, *Scomber japonicus;* (9) copper rockfish, *Sebastodes caurinus;* (10) cabezon, *Scorpaenichthys marmoratus;* staghorn sculpin, *Leptocottus armatus;* (11) sand sole, *Psettichthys melanostictus;* English sole, *Parophrys vetulus;* starry flounder, *Platichthys stellatus;* (12) northern midshipman, *Porichthys notatus.*

All antisera reacted strongly with sera from mature females within the families that provided the vitellin for antibody stimulation. Because of this high degree of cross-reactivity within families, the reactions of the antisera may be considered mainly with regard to the family rather than the species from which the vitellin used for antibody stimulation originated. The arbitrary designations given in tables 1 and 2 refer to vitellin of any species of that family.

Four of the reagents also reacted strongly beyond the immediate family group; two of them reacted distinctly with sera from mature females of all teleost species tested. Figure 1 illustrates the reactions of sera from mature female teleosts of six different families when tested with the anti-RM reagent. The strongest reaction was with the female rockfish serum. The degree of cross-reactivity regularly decreased through the somewhat distantly related salmonoids and cyprinoids. Even in these groups, however, the reaction was clear.

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[2] Trade names referred to in this publication do not imply endorsement of commercial products.

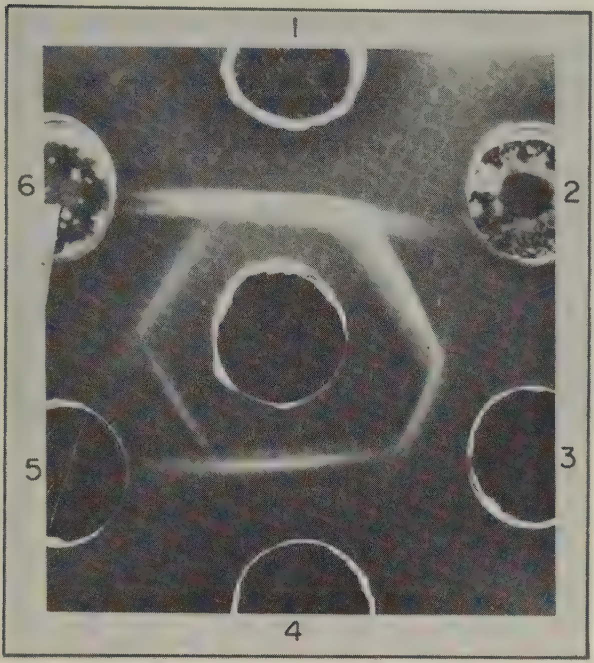

FIGURE 1.—Reactions of sera from mature females of six teleost species with rabbit anti-RM serum. Peripheral wells contain sera from 1, copper rockfish; 2, sand sole; 3, bigeye tuna; 4, Pacific cod; 5, carp; 6, sockeye salmon.

Table 3 gives the results of absorptions of the anti-RM reagent with the fish sera of figure 1. It is evident from both figure 1 and table 3 that the anti-RM reagent contains antibodies of numerous specificities.

Figure 2 presents a more detailed examination of the relationship between SM and RM vitellins. It is evident from figure 2a that the RM vitellin has at least three distinct components. The SM vitellin cross-reacts completely with the antibodies directed against one of these components. Two components are visible in figure 2b that react with the anti-SM antiserum. The RM vitellin cross-reacts partially and very weakly with the antibodies directed against one of these components.

TABLE 3.—*Results of absorptions of rabbit antirockfish vitellin (RM) serum with sera of mature female teleosts*

[X=strong reaction; W=weak reaction; 0=no reaction. See figure 1]

Fish sera used for absorption	Fish sera tested					
	Rockfish	Sole	Tuna	Cod	Carp	Salmon
Unabsorbed	X	X	X	X	X	X
Rockfish	0	0	0	0	0	0
Sole	X	0	W	0	0	0
Tuna	X	0	0	0	0	0
Cod	X	X	X	0	0	0
Carp	X	X	X	X	0	X
Salmon	X	X	X	X	0	0

Comparisons similar to those presented in figure 2 were made between the broadly cross-reactive antisera (anti-RM and anti-HM), the less cross-reactive antisera (anti-CLM, anti-SM, anti-CM, and anti-GM), and the corresponding vitellins. All results were similar. The weak or negative reactions of the RM and HM vitellins with the less cross-reactive or group-specific antisera contrasted with the strong reactions of the anti-RM and anti-HM antisera with the vitellins which elicited the less cross-reactive antisera present an interesting serological phenomenon. The cross-reactive antibodies of the anti-RM and anti-HM antisera apjear to have a considerably greater avidity for the vitellins which elicit group-specific antisera than the group-specific antibodies have for the RM and HM vitellins.

Both the homologous and cross-reaching heterologous antisera gave uniform results where tested with a larger number of individuals. Randomly selected sera from 48 sockeye salmon were tested with anto-SM, anti-RM, and anti-HM reagents; 48 halibut sera were tested with the anti-RM and anti-HM reagents. Results were identical regardless of the antiserum used, including two weak but positively reacting halibut sera.

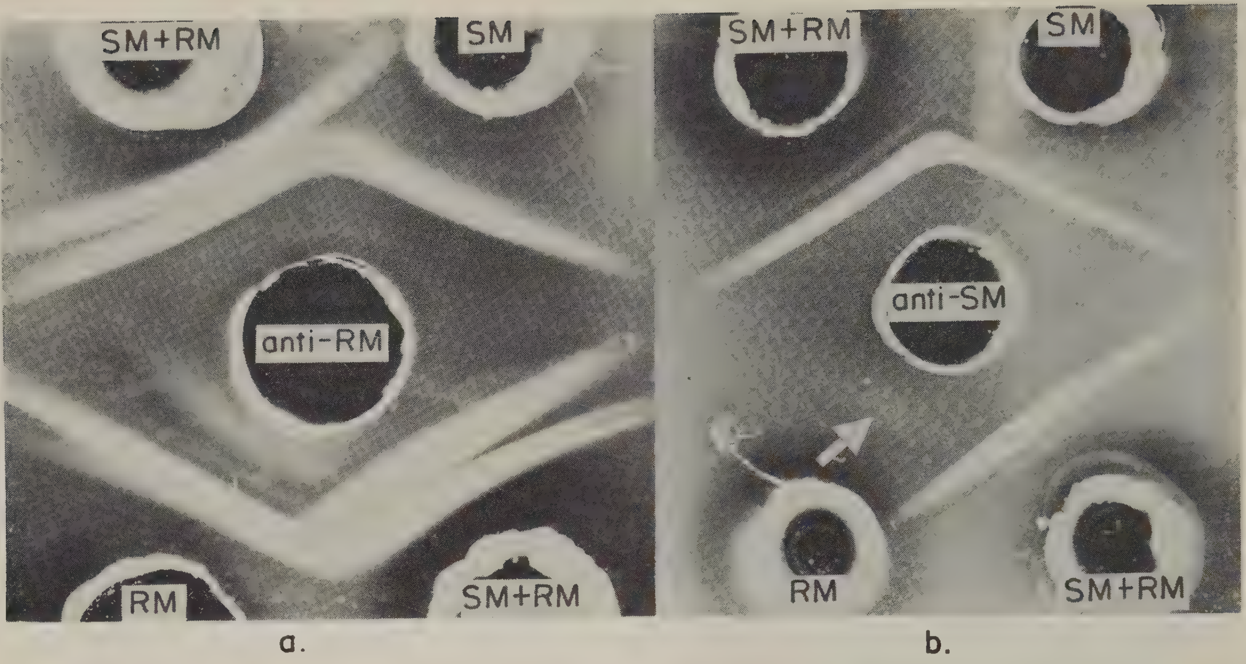

FIGURE 2.—The relation between SM and RM vitellins detected (a) by rabbit anti-RM serum and (b) by rabbit anti-SM serum. Arrow in (b) indicates the partial cross reaction between RM vitellin and the anti-SM reagent.

PRACTICAL APPLICATIONS FOR STUDIES OF MATURITY

The broad cross-reactive range of antisera produced against the vitellins of rockfish and starry flounder is of practical importance. It is likely that these reagents react with serum vitellins from mature female teleosts at least through the taxonomic range of this study. An investigator wishing to include serological data in maturity studies may therefore use a single reagent throughout a range of teleost species rather than produce different antisera for relatively limited taxonomic groupings. The necessity of obtaining vitellin-bearing material for immunizations from species where such materials would be difficult to obtain or process is also eliminated.

The data suggest that vitellins of the most taxonomically advanced species stimulate the highly cross-reactive antisera. Some theoretical implications of this apparent trend are discussed below. As a practical consideration, however, it appears that vitellin from Perciform or closely allied species may be most likely to stimulate antisera which have broad cross-reactive properties.

SYSTEMATIC CONSIDERATIONS

Nuttall (1904) in an early immunological study, observed that the quantities of precipitates formed by specific antigen-antibody interactions decrease as the taxonomic relationships become more distant from the materials used in antibody stimulation. The present study agrees generally with this observation. As illustrated by figure 1, the broadly cross-reactive antisera reacted most strongly with the homologous vitellin and least strongly with the most distantly related cpyrinid and salmonid vitellins. A notable exception is the reaction of sturgeon vitellin with anti-cyprinid vitellin, an antiserum which fails to react with vitellins of numerous, more closely related, groups. The other execptions include the weak cross-reactions of antisalmonid vitellin with rockfish vitellin but not with herring or carp vitellin, and the similarly weak cross-reaction of anticlupeid vitellin with rockfish vitellin but not with salmon vitellin.

Fine, Buffa, and Drilhon (1964) found a component in mature female marine lampreys analogous to the teleost vitellins described in this report. The spiny dogfish egg, unlike those of many sharks, is provided with an abundance of yolk material. A Saline extract of the dogfish yolk material was tested in addition to the sera from numerous adult dogfish; this extract also failed to react with any of the antisera used in this study. The lack of reactivity observed here with yolk materials from females of dogfish or lampreys appears to reflect the phylogenetic gap between the teleosts and these more primitive vertebrates.

The vitellin substances of the advanced teleosts that stimulate production of the broadly cross-reactive antisera appears to be biochemically and antigenically more complex than those of the more primitive teleosts. It is evident from figure 1 and table 3 that only a small fraction of the total number of anti-RM antibodies react with SM vitellin; the major antigenic vitellin component of SM is detected, however, by the anti-RM reagent (Figure 2). Possibly the vitellin antigens of more primitive teleost species have been retained in certain advanced species without extensive modification during the evolution of additional vitellin substances.

This study further demonstrates the usefulness of serological methods to determine maturity in oviparous vertebrates. The results are also of significance in systematics. The existence of antigens in the sera of maturing females which do not occur in the sera of males and immature females must be taken into account in studies that attempt to apply serology to problems of taxonomy. These antigens themselves, as was demonstrated here, also offer additional materials for more detailed examinations of systematic relationships.

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OCCURRENCE OF MACROZOOPLANKTON IN TAMPA BAY, FLORIDA, AND THE ADJACENT GULF OF MEXICO[1]

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ABSTRACT

This report describes a 12-month (September 1961 through August 1962) study. Plankton was collected at 14 locations with a No. 000, one-half meter net, which strained an estimated 35 m.^{3} of water per tow. Wet plankton volumes varied from $<$ 0.5 to 92.0 ml. and averaged 7.0 ml. per tow. Fifty-two percent (by volume) of the plankton was collected in the summer, 25 percent in the fall, 18 percent in the spring, and 5 percent in the winter. *Lucifer faxoni*, the most numerous organism, accounted for 18.5 percent of the total plankton volume.

Sixteen species, 24 genera, 30 families, and 21 taxonomic categories higher than family were identified. Decapod crustaceans accounted for 87 percent of the total number of zooplankters collected. The most numerous organisms, in descending order were *Lucifer faxoni*, larval porcellanids, brachyurans, chaetognaths, copepods, larval polychaetes, carideans, appendicularids, larval fish, fish eggs, thallassinids, cladocerans, and larval stomatopods. Larval forms of commercially important species were *Penaeus duorarum*, *Brevoortia* spp., *Anchoa* sp., *Trachinotus* spp., *Leiostomus xanthurus*, *Cynoscion* spp., and Soleidae.

Observed temperature ranged from 12.8° to 32.0° C. and salinity from 19.00 to 36.00 p.p.t. In relating the abundance of zooplankton to temperature and salinity the data suggested that low temperatures and salinity values were more restrictive than high ones to most of the organisms.

A study of macrozooplankton was undertaken as part of an investigation of estuarine biology in the eastern Gulf of Mexico. The primary aim was to determine temporal and spatial variations in the abundance of macrozooplankton in the surface waters of Tampa Bay and the adjacent Gulf of Mexico, and to relate the occurrence of frequently collected taxa to water temperature and salinity.

The abundance and composition of zooplankton provide an important index of biological production in estuaries, because zooplankters are the basic food of many marine organisms. Mysids, euphausids, amphipods, larval stomatopods, and fish larvae are frequent in stomachs of commercially important fishes (King, 1954). The bulk of this plankton, however, reaches large fish indirectly through their consumption of foraging organisms.

The literature on zooplankton in the coastal waters of west Florida is limited. No reports deal with the seasonal composition of zooplankton throughout Tampa Bay. Published material includes: a description of certain biological, taxonomic, and ecological aspects of the chaetognaths of the west coast of Florida (Pierce, 1951); notes on chaetognaths from the Gulf of Mexico (Tokioka, 1955); the seasonal distribution of penaeid larvae from the lower portion of Tampa Bay, Fla., and the adjacent Gulf of Mexico waters (Eldred, Williams, Martin, and Joyce, 1965); a qualitative and quantitative seasonal study of the copepods of Alligator Harbor (Grice, 1956); studies of the taxonomy of several calanoid copepods in the eastern Gulf of Mexico (Fleminger, 1957a and 1957b); a preliminary report on the plankton of the west coast of Florida with a discussion of the distribution and occurrence of copepods and other crustaceans (King, 1949); and records of various taxa from the marine and brackish waters of south Florida (Davis, 1947, 1948, 1949, 1950; Davis and Williams, 1950; and Dragovich, 1963).

DESCRIPTION OF THE AREA

Tampa Bay is a shallow embayment consisting of five sub-areas, also identified as bays—

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[1] Contribution No. 27, Bureau of Commercial Fisheries Biological Laboratory, St. Petersburg Beach, Fla.

Published April 1967.

Old Tampa Bay, Hillsborough Bay, Tampa Bay, Boca Ciega Bay, and Terra Ceia Bay. Collectively, these areas have a shoreline of 341 km. and cover an area of 896 km.[2], 90 percent of which is less than 6.7 m. deep (Olson and Morrill, 1955).[2] The principal tributaries of Tampa Bay are the Hillsborough, Alafia, Manatee, and Little Manatee Rivers. Their discharge is largely influenced by rainfall (Dragovich and May, 1962) and is subordinate to tidal exchange in the circulation of Bay water (Goodell and Gorsline, 1961).

The climate of the Bay area is subtropical. The mean monthly air temperature at Tampa, Fla., averages 22.3° C. annually and varies from 16.2° C. (January) to 27.8° C. (August)[3]. The rainy season in the Tampa Bay area usually extends from June to October. Mean rainfall varies monthly from 3.7 cm. (November) to 21.9 cm. (July) and totals 131.0 cm. annually.

APPARATUS AND METHODS

FIELD PROCEDURES

Plankton was sampled monthly in Tampa Bay and adjacent waters of the Gulf of Mexico from September 1961 through August 1962 (table 1). Surface samples were collected at 14 stations (fig. 1 and table 2) with a No. 000, ½-m., nylon plankton net (mesh size 1.024 mm.). This net was selected primarily for the collection of larval fishes and invertebrates. Tows were made at 5.6 km. per hour (3 knots) for 2 minutes and randomly with respect to tidal stage. Vessel speed was determined before sampling by clocking elapsed time over a known distance. Net-towing rates were held

TABLE 2.—*Sampling locations in Tampa Bay and the adjacent Gulf of Mexico, September 1961–August 1962*

Station	Latitude N.	Longitude W.	Area description
1	27°35.8′	82°57.1′	10 miles (18.5 km.) offshore
2	27°36.0′	82°50.0′	3½ miles (6.5 km.) offshore
3	27°35.5′	82°45.5′	Egmont Key
4	27°32.7′	82°43.7′	Lower Tampa Bay
5	27°38.8′	82°42.7′	Boca Ciega Bay
6	27°41.5′	82°44.1′	Boca Ciega Bay
7	27°42.2′	82°40.5′	Boca Ciega Bay
8	27°33.0′	82°35.7′	Terra Ceia Bay
9	27°41.3′	82°32.9′	Central Tampa Bay
10	27°47.6′	82°34.4′	Upper Tampa Bay
11	27°56.6′	82°37.0′	Central Old Tampa Bay
12	28°00.9′	82°40.7′	Upper Old Tampa Bay
13	27°48.7′	82°26.8′	Lower Hillsborough Bay
14	27°53.7′	82°26.4′	Upper Hillsborough Bay

TABLE 1.—*Dates and numbers of plankton tows in Tampa Bay and the adjacent Gulf of Mexico, September 1961 through August 1962*

Dates	Stations														All stations
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	
	Number of plankton tows														
Fall															
Sept. 18–27, 1961	1	1	1	1	1	1	1	1	1	1	1	1	1	1	14
Oct. 2–30	1	1	1	1	2	2	2	1	1	1	1	1	1	1	17
Nov. 1–30	2	2	2	1	2	2	2	2	2	2	2	3	2	2	28
Season total	4	4	4	3	5	5	5	4	4	4	4	5	4	4	59
Winter															
Dec. 11–12, 1961	2	2	2	2	2	2	2	2	2	2	2	2	2	2	28
Jan. 8–26, 1962	2	2	2	2	2	2	2	2	1	2	2	2	1	1	25
Feb. 5–10	0	0	0	0	2	2	2	0	0	1	1	2	1	1	12
Season total	4	4	4	4	6	6	6	4	3	5	5	6	4	4	65
Spring															
Mar. 8–29, 1962	1	1	1	1	2	2	2	1	1	1	1	2	1	1	18
Apr. 9–26	2	2	2	2	2	2	2	2	2	2	2	2	2	2	28
May 7–29	1	1	1	1	2	1	2	1	2	2	2	1	2	2	21
Season total	4	4	4	4	6	5	6	4	5	5	5	5	5	5	67
Summer															
Jun. 11–28, 1962	2	2	2	2	2	2	2	2	2	2	2	2	2	2	28
Jul. 9–25	2	2	2	2	2	2	2	1	2	2	2	1	2	2	26
Aug. 6–27	2	2	2	2	2	2	2	2	1	2	2	1	0	0	22
Season total	6	6	6	6	6	6	6	5	5	6	6	4	4	4	76
Total for 12 months	18	18	18	17	23	22	23	17	17	20	20	20	17	17	267

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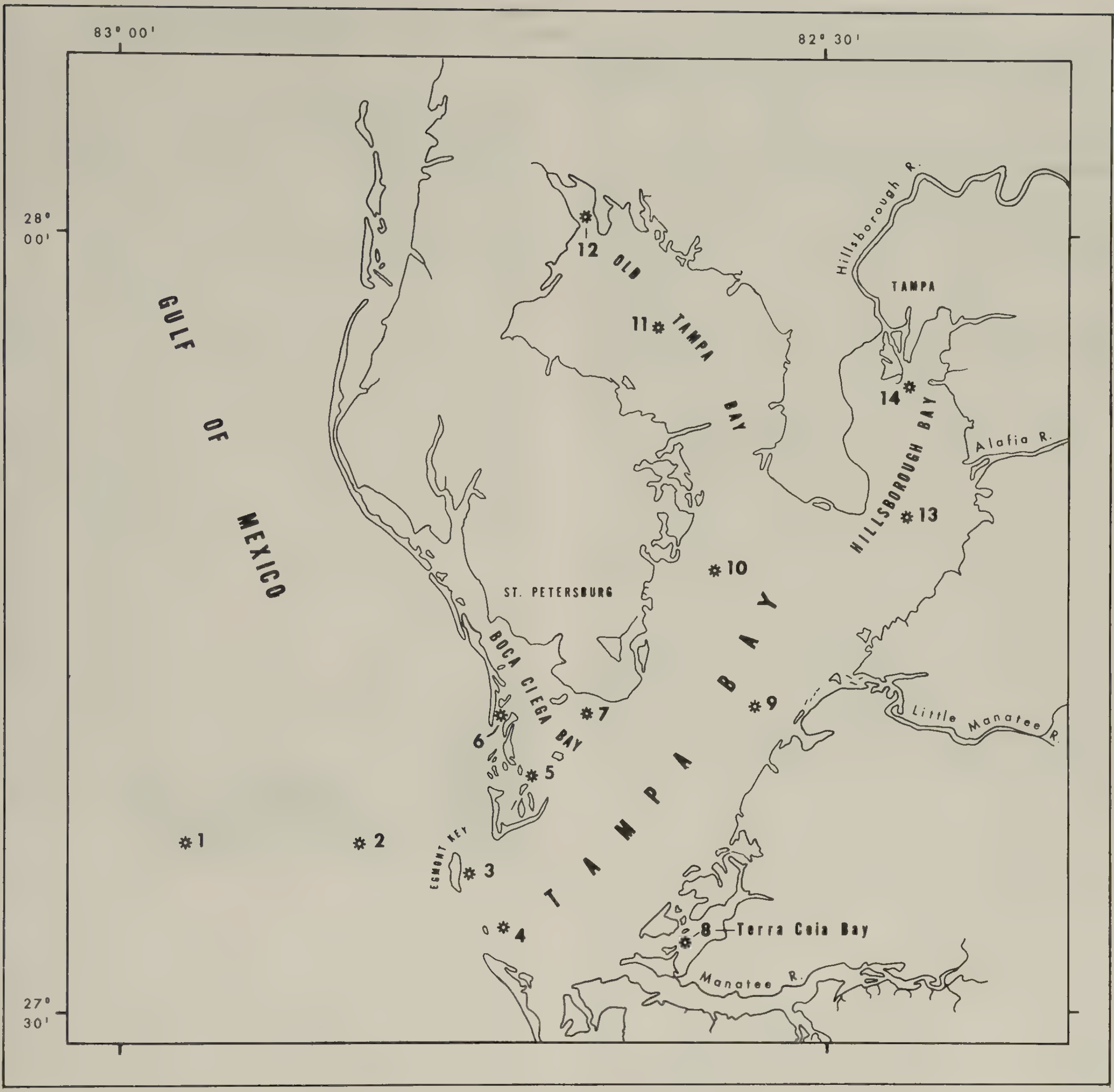
[2] Olson, F. C. W., and John B. Morrill, Jr. 1955. Literature survey of the Tampa Bay area. Armed Serv. Tech. Info. Agency, AD 81621 (Pt. 1): 66 p.p.

[3] The rainfall and temperature data used in this section are climatological normals (1931–60) compiled by the U.S. Department of Commerce, Weather Bureau, and published in the 1964 Annual Summary of Climatological Data For Tampa, Fla.


83° 00'
82° 30'
28° 00'
27° 30'
GULF OF MEXICO
OLD TAMPA BAY
TAMPA
Hillsborough R.
Alafia R.
HILLSBOROUGH BAY
ST. PETERSBURG
BOCA CIEGA BAY
TAMPA BAY
EGMONT KEY
Terra Ceia Bay
Little Manatee R.
Manatee R.
1
2
3
4
5
6
7
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9
10
11
12
13
14

FIGURE 1.—Sampling locations in Tampa Bay and the adjacent Gulf of Mexico.

nearly constant by maintaining a fixed engine speed. The volume of the cylinder of water strained through the net was determined to be 35 m.^{3} (calculated from the towing distance and the area of the net mouth). Since no correction was made to adjust for the effects of currents and clogging on the flow of water through the net, the quantitative data are not exact.

Plankton samples were preserved immediately after their collection in 5 percent neutralized formalin and stored in 30-oz. jars.

Water temperature and water sample (for salinity titration) were taken at the beginning of each plankton tow. Temperature was read to the nearest 0.1° C. with a thermister (Whitney[4] underwater thermometer, Model TC-5).

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[4] References to trade names in this publication do not imply endorsement of commercial products.

LABORATORY PROCEDURES

Plankton samples were placed in enameled photographic trays. Seaweeds and jelly fishes were removed from the samples manually, and the remaining volume was determined in the laboratory by the displacement method described by Thrailkill (1957). Plankton counts were made from aliquots whenever the wet plankton volume of the sample exceeded 0.5 ml. After the sample had been diluted to a known volume, usually 500 ml., four 5-ml. aliquots were withdrawn with a calibrated pipette. They were then transferred into a quadripartitioned petri dish for examination and counting under a binocular dissecting microscope. Samples having a wet volume of 0.5 ml. or less were transferred directly to petri dishes for counting. All samples were examined routinely for unusual organisms that might have been excluded from the aliquots. The mean number of organisms per cubic meter of water was calculated for each taxonomic group.

Body lengths of chaetognaths and fish larvae were measured-chaetognaths from the anterior extermity of the head to the tip of the caudal segment, excluding the caudal fin (Owre, 1960), and fish larvae from the snout to the base of the hypural plate (standard length).

ENVIRONMENTAL FACTORS

HYDROLOGY

The minimum and maximum water temperatures observed were 12.8° and 32.0° C. The smallest range in temperature at individual stations occurred in Boca Ciega Bay (15.3° C.), and the greatest (18.4° C.) in Old Tampa Bay (table 3). Seasonally, the range in mean temperatures between stations located on a traverse from offshore to Hillsborough Bay (stations 1, 2, 3, 4, 9, 10, 13, 14) was greatest in the spring (3.9° C.) and lowest in the winter (1.0° C.). These ranges in the fall and summer were 1.7° and 1.2° C. respectively.

Salinity was determined by Mohr-Knudsen method (Knudsen, 1901). Lowest salinities were usually in the upper area of Hillsborough Bay and highest 18.5 km. (10 nautical miles) offshore (table 3). The seasonal differences in mean salinities between these two areas (stations 1 and 14) were 8.62 p.p.t. (fall), 6.75 p.p.t. (winter), 8.03 p.p.t. (spring), and 13.58 p.p.t. (summer). The range in salinity at individual stations decreased progressively from upper Hillsborough Bay seaward. The smallest range was 18.5 km. offshore and the greatest in upper Hillsborough Bay, where temporal changes in salinity generally followed the dis-

TABLE 3.—*Mean surface water temperature and salinity for Tampa Bay and the adjacent Gulf of Mexico, September 1961 through August 1962*

Seasons	Temperature at stations													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
	° *C.*	° *C.*	° *C.*	° *C.*	° *C.*	° *C.*	° *C.*	° *C.*	° *C.*	° *C.*	° *C.*	° *C.*	° *C.*	° *C.*
Fall	24.9	24.7	24.5	26.2	24.5	24.2	23.9	25.6	25.5	24.7	24.6	23.5	24.8	25.4
Winter	17.7	17.2	17.4	17.5	17.9	18.0	18.2	18.3	17.7	17.2	17.3	18.7	17.2	18.2
Spring	21.2	21.7	22.4	22.0	21.0	19.8	20.9	23.2	22.7	23.4	23.9	21.7	24.1	25.1
Summer	29.3	30.2	30.0	30.3	30.3	30.4	29.7	30.6	30.2	29.7	30.2	30.0	30.4	30.5
12 months	24.0	24.2	24.3	24.6	23.4	23.2	23.2	24.8	24.7	24.0	24.3	22.9	24.1	24.8
Minimum	15.3	15.1	15.4	15.4	14.3	15.2	15.4	15.1	15.4	13.8	13.2	12.8	13.4	13.8
Maximum	30.9	31.2	31.4	31.4	31.9	31.4	30.7	31.5	31.6	30.6	31.6	31.2	31.2	32.0
12-month range	15.6	16.1	16.0	16.0	17.6	16.2	15.3	16.4	16.2	16.8	18.4	18.4	17.8	18.2
	Salinity at stations													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
	‰	‰	‰	‰	‰	‰	‰	‰	‰	‰	‰	‰	‰	‰
Fall	34.96	34.54	34.03	33.80	32.30	32.94	31.82	31.15	29.53	28.29	25.73	24.66	27.27	26.34
Winter	34.45	33.64	33.82	33.20	33.01	33.22	32.01	31.96	30.52	29.39	27.76	26.86	28.38	27.70
Spring	34.89	34.30	33.76	33.97	33.90	33.79	32.44	31.57	31.19	29.45	29.06	28.52	28.10	26.86
Summer	35.67	35.31	34.99	35.16	33.98	34.62	32.59	30.56	29.46	27.90	28.46	28.05	25.96	22.09
12 months	35.07	34.52	34.23	34.18	33.34	33.67	32.23	31.26	30.17	28.74	27.89	26.96	27.46	25.81
Minimum	33.96	33.04	32.63	32.74	31.29	32.38	30.05	27.63	27.45	24.78	24.11	21.82	24.36	19.00
Maximum	35.93	36.00	35.58	36.00	35.35	35.39	34.33	33.68	33.13	30.79	29.83	29.67	29.85	28.51
12-month range	1.97	2.96	2.95	3.26	4.06	3.01	4.28	6.05	5.68	6.01	5.72	7.85	5.49	9.51

charges of the Hillsborough River[5]—the major source of river water to the bay (fig. 2).

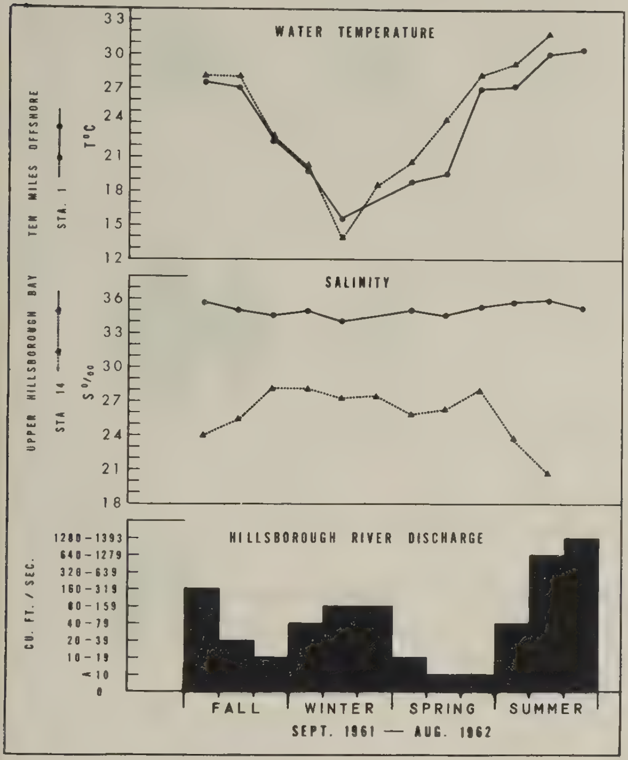

FIGURE 2.—Mean monthly discharge rate for the Hillsborough River and monthly surface water temperature and salinity for upper Hillsborough Bay (station 14) and 10 nautical miles offshore (station 1), September 1961 through August 1962. Mean values for temperature and salinity are given when two measurements of these variables were made in a month.

CLIMATOLOGY

Climatological data were taken from the records of the U.S. Weather Bureau for Tampa, Fla.

Rainfall was abnormally low during the study. From September 1961 through August 1962 total rainfall at Tampa, Fla., was 95.3 cm., 35.7 cm. below the climatological normal. Half of this amount (47.7 cm.) fell during the summer.

Mean monthly air temperatures at Tampa from September 1961 through August 1962 varied from 15.8° C. in January to 28.3° C. in July. Seasonally, mean air temperatures were 23.3° C. (fall), 16.7° C. (winter), 21.9° C. (spring), and 27.4° C. (summer).

ZOOPLANKTON VOLUMES

In 267 plankton tows, the volume of zooplankton per tow ranged from < 0.5 (considered as 0.25 ml. in all statistical treatments) to 92.0 ml. and averaged 7.0 ml. per sample. The greatest concentrations of macrozooplankton were in upper Tampa Bay, central Tampa Bay, lower Hillsborough Bay, central Old Tampa Bay, and 6.5 km. 3-½ nautical miles) offshore (fig. 3.

The abundance and composition of zooplankton varied widely by season and location. Twenty-five percent of the total volume was collected in the fall, 5 percent in the winter, 18 percent in the spring, and 52 percent in the summer (values adjusted for different numbers of tows per season). Coefficients of variation in zooplankton volume were calculated for each station to compare the areal variability of volumes (table 4). These coefficients

TABLE 4.—*Mean zooplankton volumes and the coefficients of variation of individual zooplankton volumes taken in Tampa Bay and the adjacent Gulf of Mexico, September 1961 through August 1962*

Seasons	Stations													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
	ml.	*ml.*	*ml.*	*ml.*	*ml.*	*ml.*	*ml.*	*ml.*	*ml.*	*ml.*	*ml.*	*ml.*	*ml.*	*ml.*
Fall	3.1	10.4	9.1	1.3	2.2	1.7	5.2	4.8	12.8	28.5	3.8	0.4	5.2	6.9
Winter	0.7	10.1	2.4	1.2	0.7	0.6	0.8	2.4	1.3	0.6	0.2	0.3	0.2	0.3
Spring	1.1	3.8	2.4	4.8	3.8	1.1	7.1	2.6	14.3	31.2	6.7	0.9	29.1	3.5
Summer	4.5	7.4	7.8	6.0	2.4	1.6	4.0	3.0	20.9	46.4	24.8	0.5	11.8	1.1
12 months	2.6	8.3	5.6	3.3	2.3	1.2	4.2	3.2	13.6	27.6	9.9	0.5	12.6	3.0
Minimum	<0.5	<0.5	<0.5	<0.5	<0.5	<0.5	<0.5	<0.5	<0.5	<0.5	<0.5	<0.5	<0.5	<0.5
Maximum	20.0	35.0	26.0	21.5	10.0	5.0	24.0	12.0	62.0	86.0	50.0	3.0	92.0	25.0
Coefficient of variation	170	120	130	140	110	140	140	100	120	100	150	140	170	190

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[5] River discharge data (fig. 2) and rainfall data used in this section were taken from the 1961 and 1962 Surface Water Records of Florida, Vol. 1: Streams, compiled by the U.S. Department of the Interior, Geological Survey, and from the 1961 and 1962 Annual Summaries of Local Climatological Data for Tampa, Florida, published by the U.S. Department of Commerce, Weather Bureau.

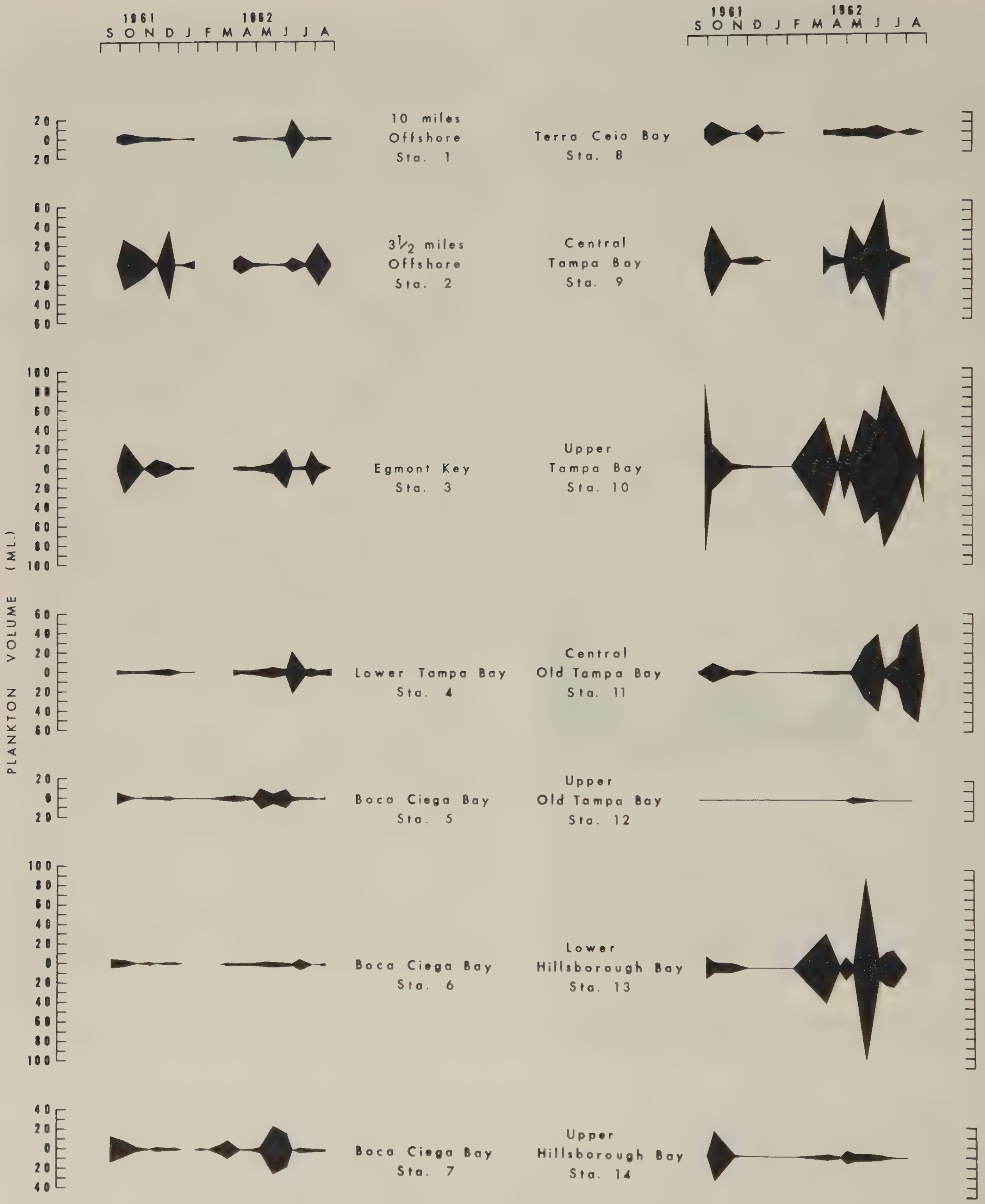

FIGURE 3.—Monthly plankton volumes for the surface waters of Tampa Bay and the adjacent Gulf of Mexico, September 1961 through August 1962. Plankton volume is expressed as milliliters per 35 m.^{3} of sea water.

varied from 100 to 190 percent. Greatest variations were at Hillsborough Bay and 18.5 km. offshore; minimum variations were in Terra Ceia Bay and in upper Tampa Bay.

CONSTITUENTS OF ZOOPLANKTON

The zooplankton consisted of holoplankton (53.5 percent), meroplankton (46.2 percent), and hypoplankton (0.3 percent). Most (87 percent) of the zooplankters in these categories were decapod crustaceans. Sixteen species, 24 genera, 30 families, and 21 taxonomic divisions higher than family were identified.

On the basis of abundance and frequency of occurrence the plankton is treated in three groups: major plankton; less abundant but frequently occurring and widely distributed organisms; and forms caught rarely.

MAJOR PLANKTON

Lucifer faxoni, larval porcellanids, and larval brachyurans, each of which accounted for 10 percent or more of the total number of organisms, were classified as major plankters. Collectively these taxa represented 83.5 percent of the zooplankton.

L. faxoni constituted 45.6 percent of the total number of zooplankters (table 5). It was the dominant zooplankter in Tampa Bay and was the only sergestid found. Most of the specimens were in the mastigopus phase, although protozoea and acanthosoma types were seen. It was collected at all stations and taken in numbers up to 1,051 per m.^{3}; 52 percent of *L. faxoni* were collected from the upper and central areas of Tampa Bay. This species was the most numerous organism in the fall, winter, and summer (fig. 4). As a result of its large size and numbers, *L. faxoni* accounted for 18.5 percent of plankton biomass. The monthly peaks in its displacement volume corresponded generally with the monthly peaks in the total volume of plankton.

Porcellanid larvae (zoea and megalops stages) formed the second most abundant group of organisms. They accounted for 27.4 percent of the total number of zooplankters and were collected in numbers up to 2,634 per m.^{3} They were most numerous in upper Tampa Bay and lower Hillsborough Bay and during the spring were the dominant organism in the area of investigation.

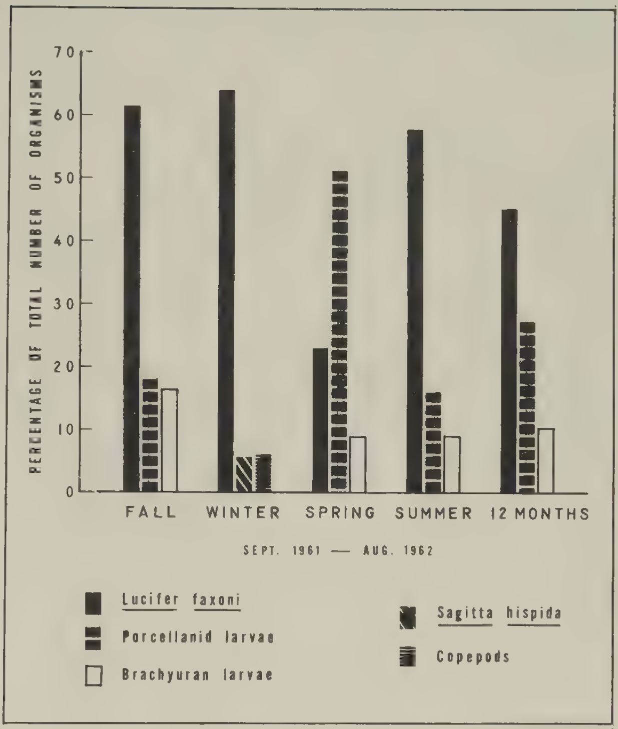

FIGURE 4.—Zooplankton taxa from Tampa Bay and the adjacent Gulf of Mexico that accounted for 5 percent or more of the organisms found during the periods shown, September 1961 through August 1962.

Except for Dromiidae, larval brachyurans were not identified to family and were classed only as zoea or megalops. Collectively they constituted 10.5 percent of the total number of zooplankters, and were the third-most-abundant taxon. Zoea and megalops were collected in numbers up to 251 per m.^{3} and 51 m.^{3} respectively. They were found at every station but appeared most abundantly in upper Tampa Bay and least abundantly in upper Old Tampa Bay. During the winter, megalops were absent at all stations in the upper portion of the area (stations 9 through 14).

In another and concurrent study, Dragovich and Kelly (1964) noted 2 species of adult Porcellanidae (*Petrolisthes galathinus* and *P. armatus*), 23 species of adult brachyurans (many of which were gravid), and a large number of juvenile portunids. Of the com-

TABLE 5.—*Frequency of occurrence and abundance (number per cubic meter in parentheses) of major zooplankters accounting for 10 percent or more of the total number of organisms collected in Tampa Bay and the adjacent Gulf of Mexico, September 1961 through August 1962*

Taxon and seasons	Frequency of occurrence and abundance per cubic meter (in parentheses)[1]								
	Stations								
	1	2	3	4	5	6	7	8	9
	No.	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
Lucifer faxoni:									
Fall	4 (1.4)	4 (107.8)	4 (56.5)	2 (3.7)	5 (21.0)	4 (15.6)	4 (50.9)	4 (29.2)	4 (343.0)
Winter	3 (1.1)	4 (145.1)	4 (14.8)	3 (11.5)	5 (1.8)	6 (2.4)	6 (7.8)	4 (24.2)	3 (44.5)
Spring	4 (4.4)	4 (55.6)	4 (17.2)	4 (14.8)	6 (16.7)	4 (1.5)	5 (61.8)	4 (15.2)	5 (97.6)
Summer	6 (2.4)	5 (75.2)	6 (23.7)	6 (39.7)	6 (51.7)	6 (19.2)	6 (75.8)	5 (10.0)	5 (273.4)
12 months	17 (2.3)	17 (93.6)	18 (27.6)	15 (20.8)	22 (22.9)	20 (9.8)	21 (49.0)	17 (19.1)	17 (197.7)
Porcellanidae:									
Fall	4 (1.4)	4 (81.4)	3 (6.0)	3 (0.8)	3 (5.5)	3 (0.5)	4 (4.6)	4 (3.5)	4 (8.8)
Winter	1 (0.1)	3 (4.1)	4 (1.2)	2 (0.8)	5 (0.9)	6 (1.3)	4 (0.4)	3 (1.2)	1 (0.2)
Spring	4 (1.2)	4 (6.4)	4 (24.2)	4 (3.8)	6 (24.4)	3 (14.4)	5 (17.9)	4 (30.2)	5 (85.0)
Summer	4 (0.3)	5 (5.9)	6 (72.5)	6 (4.2)	6 (4.9)	5 (3.4)	5 (3.8)	5 (25.4)	4 (6.0)
12 months	13 (0.7)	16 (22.4)	17 (31.2)	15 (2.7)	20 (9.1)	17 (4.7)	18 (6.8)	16 (15.7)	14 (28.8)
Brachyura:									
Fall	4 (2.1)	4 (34.6)	4 (3.9)	3 (4.7)	5 (23.8)	4 (5.7)	5 (38.2)	4 (39.9)	4 (17.0)
Winter	3 (0.4)	3 (3.1)	4 (1.2)	2 (1.9)	3 (0.6)	5 (0.8)	4 (1.0)	4 (1.1)	1 (0.3)
Spring	4 (3.0)	3 (8.2)	4 (8.2)	4 (7.2)	6 (5.1)	2 (1.8)	5 (8.2)	4 (30.1)	5 (35.0)
Summer	6 (3.3)	6 (19.9)	6 (19.5)	6 (8.8)	6 (4.2)	6 (15.9)	6 (7.5)	5 (6.8)	5 (11.2)
12 months	17 (2.3)	16 (16.9)	18 (9.5)	15 (6.1)	20 (7.8)	17 (6.2)	20 (12.6)	17 (18.7)	15 (17.6)

Taxon and seasons	Frequency of occurrence and abundance per cubic meter (in parentheses)[1]						Percentage of total number of organisms collected	Maximum abundance
	Stations					All stations		
	10	11	12	13	14			
	No.	*No.*	*No.*	*No.*	*No.*	*No.*	%	*No./m.*^{3}
Lucifer faxoni:								
Fall	4 (315.2)	4 (38.6)	2 (0.3)	4 (40.5)	4 (138.6)	53 (80.2)	61.6	1051
Winter	2 (4.8)	3 (1.0)	0 (0)	3 (0.8)	2 (1.1)	48 (15.8)	64.3	566
Spring	5 (167.4)	5 (11.3)	1 (0.2)	5 (174.6)	4 (7.0)	60 (47.7)	23.2	788
Summer	6 (492.5)	6 (107.3)	3 (0.4)	3 (97.2)	3 (8.0)	72 (94.3)	58.1	826
12 months	17 (253.8)	18 (43.0)	6 (0.2)	15 (83.9)	13 (36.8)	233 (60.4)	45.6	
Porcellanidae:								
Fall	4 (9.6)	1 (0.1)	1 (0.1)	4 (3.9)	4 (7.9)	46 (9.2)	7.1	283
Winter	2 (0.3)	3 (0.3)	0 (0)	3 (0.4)	2 (0.4)	39 (0.8)	3.3	14
Spring	5 (386.0)	5 (8.2)	4 (1.1)	4 (774.6)	5 (44.6)	62 (105.8)	51.5	2634
Summer	6 (128.5)	5 (7.7)	4 (0.8)	4 (104.2)	4 (14.6)	69 (26.6)	16.3	471
12 months	17 (137.0)	14 (4.4)	9 (0.4)	15 (253.4)	15 (18.5)	216 (36.4)	27.4	
Brachyura:								
Fall	4 (65.4)	3 (26.2)	1 (0.2)	4 (17.9)	4 (23.4)	53 (21.6)	16.6	202
Winter	3 (0.4)	3 (0.3)	0 (0)	2 (0.4)	3 (0.4)	40 (0.8)	3.3	11
Spring	5 (109.8)	5 (18.1)	2 (4.7)	5 (17.4)	4 (1.6)	58 (18.6)	9.1	236
Summer	6 (61.3)	6 (28.1)	3 (2.0)	2 (4.5)	3 (3.5)	72 (15.0)	9.2	262
12 months	18 (59.0)	17 (18.3)	6 (1.6)	14 (10.5)	13 (6.9)	223 (13.9)	10.5	

[1] See table 1 for number of samples collected.

mercially important species they caught *Callinectes sapidus* and *Menippe mercenaria.*

LESS ABUNDANT BUT WIDELY DISTRIBUTED AND FREQUENTLY OCCURRING ORGANISMS

This group of organisms consisted of taxa that occurred in 10 percent or more of the samples (table 6). Collectively they accounted for 14 percent of the total number of zooplankters. Most taxa in this category appeared during every season.

Copepods were the fourth-most-numerous group collected. They occurred in highest numbers in the spring, and were the third-most-abundant taxon in the winter (fig. 4). Because of the coarse mesh of the plankton net, only larger specimens were retained consistently. Some of the nauplius and copepodite stages and smaller adults were held in the net only when trapped among larger plankton and detritus. *Labidocera aestiva* appeared to be the dominant form. The caligoids formed only a small part (1.8 percent) of this group.

Caridean shrimp constituted 2.4 percent of the zooplankters. Most of the specimens were advanced postlarvae and were classified only to family. Identified palaemonids were represented by the subfamilies Palaemoninae and Pontiniinae and the genera *Palaemonetes* and *Periclimines;* alpheids were represented by *Alpheus* and *Synalpheus* and hippolytides by *Tozeuma, Hippolysmata,* and *Latreutes fucorum. Tozeuma* ssp., found in stages from mysis to adult, accounted for 64 percent of the hippolytides. *Hippolysmata* sp. appeared only as advanced postlarvae and *Latreutes fucorum* only as adults.

Thalassinids were mostly advanced postlarval stages. Larvae of *Upogebia* sp. and *Callianassa* sp. also appeared in the samples. Some of these larvae possibly were *Upogebia affinis* and *Callianassa atlantica,* for both species are found in Tampa Bay.

Larval stomatopods were collected at every station during the summer. Antizoea, pseudozoea, erichtus, and alima types were in most of the samples. Possibly many of the larvae were *Squilla empusa,* a prominent organism in Tampa Bay (Dragovich and Kelly, 1964).

Twelve percent of the amphipods belonged to the suborder Caprellidea; the remainder belonged to one of the suborders, Gammaridea or Hyperiidea.

TABLE 6.—*Frequency of occurrence of zooplankters found in 10 percent or more of the samples from Tampa Bay and the adjacent Gulf of Mexico (excluding the three most abundant forms shown in Table 5), September 1961 through August 1962*

[Number of tows shown in parentheses]

Taxon	Frequency of occurrence [1]																				Percentage of total number of organisms collected	Maximum abundance
	During 12 months	Season [1]				Stations																
		F	W	S	S	1	2	3	4	5	6	7	8	9	10	11	12	13	14		
	(267)	(59)	(65)	(67)	(76)	(18)	(18)	(18)	(17)	(23)	(22)	(23)	(17)	(17)	(20)	(20)	(20)	(17)	(17)		
Annelida:	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	%	*No./m.*^{3}
Terebellidae	47	6	4	12	25	0	3	8	8	9	4	0	1	0	4	6	0	4	0	1.8	128.0
Spionidae	42	9	11	8	14	1	3	4	2	3	2	0	11	0	4	7	1	4	0	0.4	46.0
Arthropoda:																					
Copepoda	177	38	42	45	52	2	15	17	15	16	12	9	15	13	19	16	4	14	10	2.7	188.0
Palaemonidae	158	35	30	52	41	13	4	12	11	20	13	13	17	8	11	14	8	11	3	1.3	37.0
Alpheidae	116	31	13	36	36	16	8	12	8	6	5	11	13	5	11	8	5	5	3	0.6	11.0
Stomatopoda	89	12	9	36	32	6	8	15	7	4	2	5	6	6	13	7	1	2	7	0.4	37.0
Hippolytidae	85	21	10	25	29	2	2	7	8	14	6	8	11	4	9	7	2	3	2	0.5	23.0
Thalassinidea	79	19	12	24	24	8	5	1	5	9	5	2	14	1	7	13	3	5	1	0.8	28.0
Amphipoda	48	7	17	15	9	0	1	3	4	12	6	1	6	2	5	4	3	1	0	0.1	3.0
Isopoda	35	7	13	7	8	2	0	0	0	2	2	2	6	0	1	1	13	2	4	<0.1	1.0
Penaeidae	26	4	1	1	20	5	4	1	2	2	5	1	1	0	2	1	1	1	0	0.2	34.0
Chaetognatha:																					
Sagitta hispida	133	24	31	38	40	9	12	16	15	10	8	10	13	7	11	9	6	3	4	1.2	34.0
Sagitta spp.[2]	107	19	11	34	43	6	11	8	12	11	7	8	9	8	10	6	4	5	2	1.2	97.0
Chordata:																					
Fish eggs	85	9	21	27	28	17	4	9	9	8	6	6	7	5	10	4	0	0	0	1.0	177.0
Appendiculariidae	83	18	13	27	25	4	9	10	11	10	4	0	14	3	4	7	0	7	0	1.3	37.0
Engraulidae	50	3	2	17	28	1	1	2	0	2	5	9	4	1	7	6	1	6	5	0.4	23.0
Sciaenidae	42	2	7	21	12	5	2	3	3	6	4	4	5	0	4	2	3	1	0	0.1	1.0
Clupeidae	39	3	15	19	2	3	5	2	0	8	8	5	2	1	2	0	2	1	0	0.1	3.0
Syngnatheidae	28	7	4	7	10	0	0	3	4	2	5	3	2	0	6	1	1	0	1	<0.1	0.5

[1] Fall, winter, spring, and summer.

[2] Immature *Sagitta* less than 5 mm long.

Most of the isopods were free-swimming cymothoids and were grouped in the genus *Aegathoa.*

Penaeids were represented by small numbers of larvae of *Sicyonia* spp., *Trachypeneus* spp., and *Penaeus duorarum; Sicyonia* (mainly mysis I and mysis III stages) constituted 36 percent of this family. They were restricted to the offshore area and lower areas of Tampa Bay (stations 1-4). Only two samples contained *Trachypeneus* larvae. The pink shrimp, *P. duorarum,* contributed 16 percent of the total penaeids. Postlarvae III stages of *P. duorarum* appeared most frequently; only occasional postlarvae I and II and mysis III were taken. These larvae were most abundant in the summer and were collected primarily in Boca Ciega Bay (station 6) and the immediately adjacent Gulf waters. Our observation of the temporal occurrence of larval stages of pink shrimp in Tampa Bay agrees generally with the findings of Eldred et al. (1965).

Appendicularia spp. and *Oikopleura* spp. were common appendiculariids and were found at most of the sampling locations.

A number of eggs and larval fish were collected. Many of the fishes were identified as commercially important species. The role of Tampa Bay in the production of species important in Gulf fisheries was discussed by Sykes and Finucane (1965).

Fish eggs were taken most frequently 18.5 km. offshore, but were most abundant at Egmont Key where 54 percent of the total number were collected. They were not identified.

Larval fish accounted for 0.8 percent of the total number of zooplankters. All engraulids were identified as *Anchoa* spp. Identified sciaenids were *Cynoscion* spp. and *Leiostomus xanthurus.* Larvae of *L. xanthurus,* 6 to 15 mm. long, were taken from late fall through early spring in Boca Ciega Bay and 6.5 km. offshore. *Cynoscion* spp. appeared infrequently during the spring and summer at most of the bay stations but were not found in Hillsborough Bay or offshore. Seventy-seven percent of the clupeids (3 to 20 mm. long) were identified as *Brevoortia.* All syngnathid larvae (5 to 44 mm. long) were of the genus *Syngnathus.*

Chaetognaths made up 3 percent of the total number of zooplankters. All undamaged specimens more than 5 mm. long were identified as *Sagitta. S. hispida* was the only chaetognath found throughout the area of investigation. It was plentiful in all seasons and was the second most abundant taxon during the winter (fig. 4). The broad dispersal and numerical abundance of immature *Sagitta* less than 5 mm. long suggest that *Sagitta* breed both in Tampa Bay and the adjacent offshore waters. The smallest chaetognath was 2.5 mm. long, but it is likely that smaller ones escaped through the net.

Polychaete larvae made up 2.4 percent of the total number of zooplankters. Terebellids (0.4 to 4 mm. long) were numerous in samples that contained a high proportion of *Bellerochea malleus.* The gut always contained large quantities of chlorophyll. None was identified to genus. Spionids (0.4 to 4 mm. long) were collected at 11 to the 14 sampling locations, but the genera *Polydora* and *Prionospio* were collected only off Egmont Key, in Boca Ciega Bay (station 6), and in Terra Ceia Bay.

FORMS RARELY CAUGHT

This group of organisms consisted of taxa which were in less than 10 percent of the samples (table 7). Only 10 of these taxa accounted for 0.1 percent or more of the total number of zooplankters, though many of them (e.g. pagurids, mollusks, and echinoderms) are common as adults of this area. The paucity of planktonic stages in this study may be ascribed partially to the large mesh of the collecting net and to the fact that only surface samples were taken.

The areal distribution of most of the plankters in this group was limited. Most of the cladocerans (66 percent), cirripedians (61 percent), and lancelets (60 percent) were collected in one sample taken during May from lower Hillsborough Bay. Fifty-three percent of the pagurids were taken in August in a single sample from upper Tampa Bay. Forty-two percent of the larval blennies were collected from the same area; they were present throughout the year but were most abundant in September. *Sagitta helenae* and *S. enflata* occurred fre-

TABLE 7.—*Frequency of occurrence of zooplankters found in less than 10 percent of the samples from Tampa Bay and the adjacent Gulf of Mexico, September 1961 through August 1962*

[Number of tows shown in parentheses]

Taxon	Frequency of occurrence [1]																			Percentage of total number of organisms collected	Maximum abundance
	During 12 months	Season [1]				Stations															
		F	W	S	S	1	2	3	4	5	6	7	8	9	10	11	12	13	14		
	(267)	(59)	(65)	(67)	(76)	(18)	(18)	(18)	(17)	(23)	(22)	(23)	(17)	(17)	(20)	(20)	(20)	(17)	(17)		
Aschelminthes:	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	%	*No./m.*^{3}
Nematoda	2	-----	-----	2	-----	-----	-----	-----	-----	1	-----	-----	-----	-----	1	-----	-----	-----	-----	<0.1	1.0
Mollusca:																					
Gastropoda	17	5	9	1	2	-----	2	4	2	1	2	-----	4	-----	-----	1	1	-----	-----	<0.1	3.0
Pelecypoda	1	-----	-----	-----	1	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	1	-----	-----	-----	<0.1	0.5
Annelida:																					
Syllidae	9	1	3	2	3	-----	-----	3	-----	2	1	1	-----	-----	1	1	-----	-----	-----	<0.1	6.0
Nereidae	4	2	-----	-----	2	-----	1	-----	-----	1	-----	-----	-----	-----	1	1	-----	-----	-----	<0.1	3.0
Phyllodocidae	4	1	1	1	1	-----	-----	1	1	1	-----	-----	1	-----	-----	-----	-----	-----	-----	<0.1	1.0
Poecilochaetidae	3	-----	-----	3	-----	-----	-----	1	-----	-----	-----	-----	-----	-----	2	-----	-----	-----	-----	<0.1	0.5
Sabellidae	2	-----	1	-----	1	-----	-----	-----	-----	2	-----	-----	-----	-----	-----	-----	-----	-----	-----	<0.1	1.0
Polynoidae	1	-----	1	-----	-----	-----	1	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	<0.1	0.5
Polychaetes (unidentified)	5	3	-----	1	1	1	-----	1	-----	1	-----	1	-----	-----	-----	1	-----	-----	-----	0.1	17.0
Arthropoda:																					
Paguridae	21	4	6	6	5	-----	-----	3	-----	-----	1	1	7	1	6	-----	1	-----	1	0.1	8.0
Cladocera	17	3	3	4	7	-----	3	6	2	1	-----	-----	2	-----	1	-----	-----	2	-----	0.8	217.0
Cirripedia	7	-----	2	4	1	-----	-----	1	1	1	-----	-----	1	-----	-----	-----	-----	3	-----	0.1	28.0
Cumacea	4	-----	2	-----	2	-----	1	-----	1	-----	-----	-----	1	-----	-----	1	-----	-----	-----	<0.1	3.0
Scyllaridea	4	2	-----	-----	2	1	-----	2	-----	-----	-----	-----	1	-----	-----	-----	-----	-----	-----	<0.1	0.5
Hippidae	3	2	-----	-----	1	1	1	-----	-----	-----	-----	-----	-----	-----	1	-----	-----	-----	-----	<0.1	8.0
Ostracoda	3	-----	2	-----	1	-----	-----	-----	-----	-----	-----	-----	2	-----	-----	1	-----	-----	-----	<0.1	0.5
Processidae	2	-----	1	1	-----	-----	-----	-----	-----	1	-----	-----	-----	-----	1	-----	-----	-----	-----	<0.1	6.0
Mysidacea	2	1	-----	1	-----	-----	-----	-----	-----	2	-----	-----	-----	-----	-----	-----	-----	-----	-----	<0.1	1.0
Euphausiacea	2	1	1	-----	-----	1	-----	1	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	<0.1	1.0
Dromiacea	2	1	-----	-----	1	2	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	<0.1	0.5
Pycnogonida	1	-----	1	-----	-----	-----	-----	-----	-----	-----	1	-----	-----	-----	-----	-----	-----	-----	-----	<0.1	0.5
Chaetognatha:																					
Sagitta helenae	24	3	5	6	10	17	4	1	1	-----	-----	-----	-----	1	-----	-----	-----	-----	-----	0.2	30.0
Sagitta enflata	13	4	4	1	4	12	-----	1	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	0.1	16.0
Sagitta tenuis	8	2	-----	2	4	6	-----	-----	-----	1	-----	-----	-----	-----	-----	-----	-----	1	-----	<0.1	2.0
Echinodermata:																					
Holothuroidea	1	1	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	1	-----	-----	-----	<0.1	3.0
Ophiuroidea	1	-----	-----	-----	1	-----	-----	-----	-----	-----	1	-----	-----	-----	-----	-----	-----	-----	-----	<0.1	0.5
Chordata:																					
Blenniidae	25	3	1	20	1	-----	-----	1	1	1	4	1	3	2	6	3	1	2	-----	0.1	7.0
Carangidae	15	3	-----	-----	12	-----	-----	2	1	1	2	1	-----	-----	4	4	-----	-----	-----	<0.1	0.5
Branchiostomidae	8	-----	1	4	3	-----	1	1	1	-----	-----	-----	4	-----	-----	-----	-----	1	-----	0.1	23.0
Thaliacea	8	3	1	2	2	6	2	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	<0.1	3.0
Soleidae	8	1	-----	2	5	-----	-----	-----	-----	3	1	2	-----	-----	1	1	-----	-----	-----	<0.1	1.0
Triglidae	7	1	-----	3	3	-----	-----	2	-----	-----	2	-----	-----	-----	2	1	-----	-----	-----	<0.1	6.0
Gerridae	4	1	-----	-----	3	-----	-----	-----	1	-----	1	2	-----	-----	-----	-----	-----	-----	-----	<0.1	1.0
Gobiidae	4	1	1	2	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	2	2	-----	-----	<0.1	0.5
Belonidae	2	-----	-----	-----	2	-----	-----	-----	-----	-----	2	-----	-----	-----	-----	-----	-----	-----	-----	<0.1	0.5
Atherinidae	2	-----	-----	1	1	-----	-----	-----	-----	-----	-----	-----	1	-----	-----	1	-----	-----	-----	<0.1	0.5
Cynoglossidae	1	-----	1	-----	-----	-----	-----	-----	-----	-----	-----	1	-----	-----	-----	-----	-----	-----	-----	<0.1	0.5
Fish larvae (unidentified)	38	4	8	10	16	5	2	3	4	1	-----	4	1	4	5	4	1	1	3	0.1	3.0

[1] Fall, winter, spring, and summer.

quently 18.5 km. offshore where they accounted respectively for 25 and 8 percent of the zooplankters collected in that area.

Forms identified in the samples but not included in the aliquots of samples that were counted were: the euphausiacean (*Euphausia americana*); cumacean (*Oxyurostilis* sp.); decapods (*Scyllarus* sp., *Emerita talpoida*, and *Dromidia antillensis*); lancelet (*Brachiostoma caribeum*); larval fish (*Strongilura timucu*, and *Prionotus* sp.); and polychaetes (*Nereis* sp., *Platynereis dumerilii*, and *Poecilochaetus johnsoni*). The present collection represents the first record of larval *P. johnsoni* from the southeastern United States (Taylor, 1966).

OCCURRENCE OF ZOOPLANKTON IN RELATION TO TEMPERATURE AND SALINITY

TEMPERATURE

To relate water temperature with the occurrence of the most plentiful zooplankton—22 taxa accounting for 98 percent of the total number of zooplankters collected — the temperature data were divided into three ranges (12.8° to 20.9° C., to 21.0° to 27.9° C., and 28.0° to 32.0° C.), each of which included about an equal number of temperature observations (table 8). Occurrences of plankton were adjusted for the differences in numbers of temperature observations in each range and ex-

TABLE 8.—*Percentage frequency of occurrence (adjusted for the difference in numbers of temperature and salinity observations in each range) of the most plentiful zooplankton at three salinity and temperature intervals, each of which includes about an equal number of observations—Tampa Bay and the adjacent Gulf of Mexico, September 1961 through August 1962*

Taxon	Total occurrences	Temperature (° C.)[1]			Salinity (‰)[1]		
		12.8–20.9 (89)	21.0–27.9 (96)	28.0–32.0 (82)	19.0–29.4 (90)	29.5–33.4 (89)	33.5–36.0 (88)
	No.	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
Annelida:							
Terebellidae	47	16.6	27.0	56.4	23.0	19.1	57.9
Spionidae	42	30.8	30.7	38.5	30.6	45.3	24.1
Arthropoda:							
Lucifer faxoni	233	29.6	34.6	35.8	27.6	36.4	36.0
Brachyura	223	28.1	33.6	38.3	28.8	34.0	37.2
Porcellanidae	216	30.5	32.5	37.0	31.6	31.9	36.5
Copepoda	177	33.2	30.2	36.6	33.0	32.7	34.3
Palaemonidae	158	31.6	33.3	35.1	30.0	36.7	33.3
Alpheidae	116	25.8	34.2	40.0	23.0	34.4	42.6
Stomatopoda	89	25.7	34.3	40.0	26.7	30.2	43.1
Hippolytidae	85	24.4	29.0	46.6	23.2	43.5	33.3
Thalassinidea	79	21.3	32.5	46.2	32.6	34.2	33.2
Amphipoda	48	39.8	35.1	25.1	22.6	43.7	33.7
Isopoda	35	31.7	43.0	25.3	62.6	25.9	11.5
Penaeidae	26	3.6	16.9	79.5	19.0	11.6	69.4
Chaetognatha:							
Sagitta hispida	133	32.8	29.1	38.1	20.0	39.0	41.0
Sagitta, spp.[2]	107	26.6	24.6	48.8	23.1	32.6	44.3
Chordata:							
Fish eggs	85	37.7	31.6	30.7	13.9	35.1	51.0
Appendiculariidae	83	31.2	31.1	37.7	20.2	36.0	43.8
Engraulidae	50	13.8	32.9	53.3	45.6	32.1	22.3
Sciaenidae	42	43.0	31.1	25.9	18.8	42.7	38.5
Clupeidae	39	60.6	36.6	2.8	10.0	53.8	36.2
Syngnatheidae	28	24.8	29.5	45.7	24.7	39.2	36.1

[1] Total number of temperature and salinity observations within each range shown in parentheses.

[2] Immature *Sagitta* less than 5 mm. long.

pressed as percentage frequency of occurrence. Seventeen of the taxa occurred most frequently at the highest range, one at the intermediate range, and four at the lowest range. These observations suggest that for most zooplankton low temperatures were more restrictive than high.

SALINITY

The study of the relation of salinity to the occurrence of zooplankton was similar to that for temperature. The salinity ranges used were 19.0 to 29.4 p.p.t., 29.5 to 33.4 p.p.t., and 33.5 to 36.0 p.p.t. (table 8). Eleven of the 22 taxa occurred most frequently at the highest range, nine at the intermediate range, and two at the lowest range. These comparisons suggest that low salinity restricts the distribution of zooplankton in Tampa Bay.

The zooplankton included both euryhaline and marine forms. *Lucifer faxoni*, porcellanids, copepods, and chateognaths were taken throughout the entire salinity range (19.0 to 36.0 p.p.t.). The range for *L. faxoni* was similar to the range (19.3 to 34.2 p.p.t.) given by Woodmansee (1958) in Biscayne Bay, Fla.

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THE GEOSTROPHIC CIRCULATION AND DISTRIBUTION OF WATER PROPERTIES OFF THE COASTS OF VANCOUVER ISLAND AND WASHINGTON, SPRING AND FALL 1963

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ABSTRACT

Analysis of oceanographic data collected during the spring and fall cruises of the RV *George B. Kelez* in 1963 within 220 kilometers of the coasts of Vancouver Island and Washington indicated a net volume transport toward the north; the flow was about 3 x 10^6m.^{3} sec. off northern Vancouver Island, but only 1 x 10^6m.^{3}/sec. off Washington.

The major structural features were consistent in each of the nine vertical sections of salinity, temperature, or dissolved oxygen normal to shore between the Columbia River and Cape Cook.

A water mass that had higher salinity, higher temperature, and lower dissolved-oxygen concentration than offshore water existed over the continental slope below the halocline. The implied northward flow at depth along the coast was very weak. These data add to the increasing body of information concerning the California Undercurrent.

At a conference on fishery-oceanography at San Francisco, Calif., on June 2, 1947, the need became obvious for repeated oceanographic surveys along the Pacific coast up to about 500 km. offshore (Sette, 1947). A gap existed at the time of this conference between proposed sampling off the California coast by Scripps Institution of Oceanography and off the Canadian coast by the Pacific Oceanographic Group. This gap narrowed when the Department of Oceanography, at Oregon State University, began a survey of Oregon coastal waters in June 1958, and the Department of Oceanography at the University of Washington in January 1961 began a study of the area influenced by the Columbia River effluent. Extensive oceanographic observations from the Columbia River to northern Vancouver Island in the spring and fall of 1963, by the Oceanographic Section of the Bureau of Commercial Fisheries Biological Laboratory, Seattle, Wash., also filled in a portion of the gap. The purpose of the spring cruise was to determine oceanographic conditions in the coastal environment within 185 km. of shore (Ingraham, 1964); the fall cruise was planned to determine whether significant changes had occurred since spring. The locations of oceanographic stations for both cruises are shown in figure 1.

This report presents the significant features of the distributions of salinity, temperature, dissolved oxygen, and water mass and the circulation as shown by geostrophic currents at the surface and at 200 meters.

CIRCULATION

Interesting aspects of the circulation close to the coast are the extent, continuity, and source of the surface Davidson Current and of the subsurface California Undercurrent, and the relationship of the two. The flow in the Davidson Current has been clearly shown by drift bottles released during fall, winter, and early spring from as far south as central California and recovered along the coast of British Columbia. This surface current extends at least 93 km. from shore; it usually has an average speed of about 15 cm./sec. but speeds of about 40 cm./sec. have been found (Schwartzlose, 1963). Burt and Wyatt (1964) reported similar minimal velocities for drift bottles released off Oregon during January 1961 and recovered off Vancouver Island.

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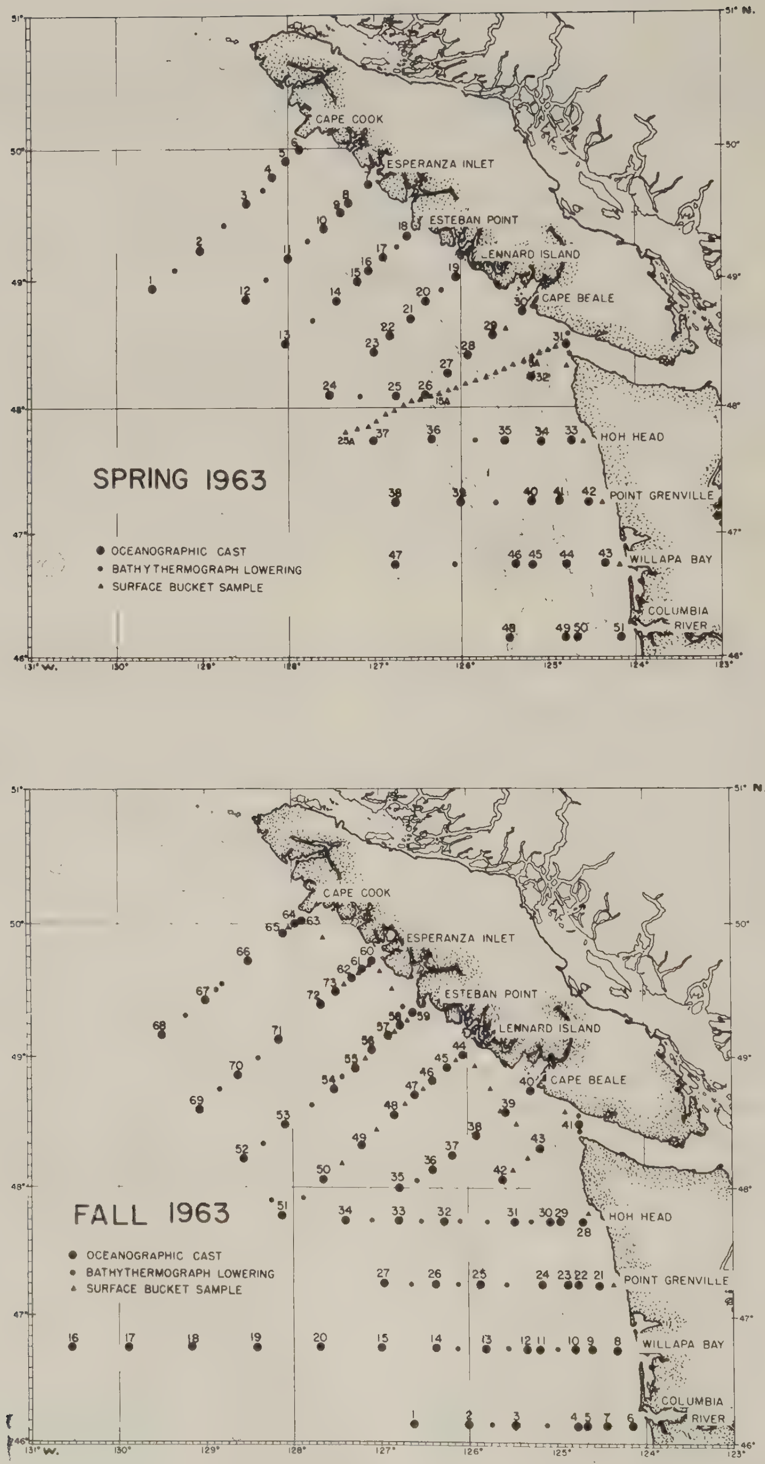
SPRING 1963
CAPE COOK
ESPERANZA INLET
ESTEBAN POINT
LENNARD ISLAND
CAPE BEALE
HOH HEAD
POINT GRENVILLE
WILLAPA BAY
COLUMBIA RIVER
● OCEANOGRAPHIC CAST
• BATHYTHERMOGRAPH LOWERING
▲ SURFACE BUCKET SAMPLE
FALL 1963
51° N.
50°
49°
48°
47°
46°
131° W.
130°
129°
128°
127°
126°
125°
124°
123°

FIGURE 1.—Locations of oceanographic stations, RV *George B. Kelez*, April 30, to May 17 and October 23 to November 24, 1963. (The 183- and 1,829-m. depth contours are shown.)

The cause of the Davidson Current is not clearly understood. Off the coast of Oregon it appears to result from local wind stress, but direct measurements during October 1958 and January 1959 (Reid and Schwartzlose, 1963) indicate that the driving force of this current is not local winds; it may be a surface manifestation of a deeper northward-flowing countercurrent that develops when winds weaken seasonally (Sverdrup, Johnson, and Fleming, 1942). This northward countercurrent which opposes the offshore California Current has been reported off central California below 200 m. throughout the year (Reid, Roden, and Wyllie, 1958). Northward flow also was reported off Washington and Oregon below 200 m. during the summers of 1955–57 and 1959; this report was based upon limited observations (Dodimead, Favorite, and Hirano, 1963). Our closely spaced observations during 1963 permit a more detailed evaluation of the size and continuity of the surface Davidson Current, the subsurface California Undercurrent, and other major features of the circulation off the coasts of British Columbia and Washington.

GEOSTROPHIC CURRENTS

Geostrophic currents reflect the general circulation associated with the distribution of mass. They are calculated from an arbitrarily selected reference depth and are, therefore, relative currents. The 1,000-db. (decibar) surface has been used as a reference surface in the North Pacific Ocean by Reid (1961), Dodimead et al. (1963), Budinger, Coachman, and Barnes (1964), and Favorite (1966) because they had

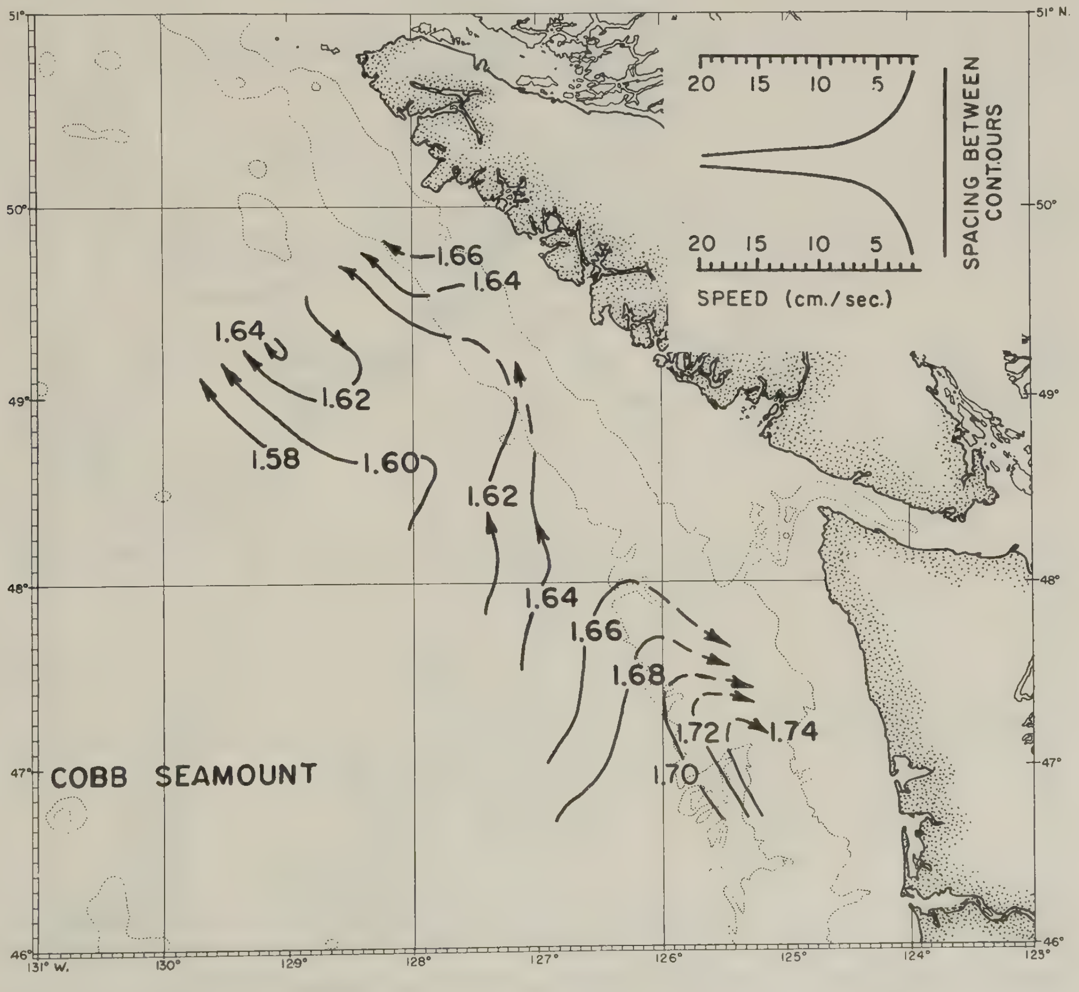

FIGURE 2.—Geopotential topography, 0/1,500 m., spring 1963. (The 183- and 1,829-m. depth contours are shown.)

sufficient data only to 1,000 m. Bennett (1959), using a deeper reference level, obtained greater surface velocities for the Gulf of Alaska. In the absence of a known depth of no motion, the deepest level compatible with all the data (1,500 db.) was selected for the reference surface in this study. Other assumptions that limit the accuracy of geostrophic currents are: (1) synoptic data, (2) unaccelerated flow, (3) lack of internal wave or tidal influence, and (4) absence of friction.

Caution must be used in the estimation of the surface velocity from geostrophic currents alone. The Ekman Current (Sverdrup et al., 1942) caused by local, variable wind stress must be added to the geostrophic current, for it is reasonable to assume in the absence of direct measurements of current that the Ekman velocities at the surface may exceed the surface geostrophic velocities. Examination of transport values computed from mean monthly pressure charts (Fofonoff and Ross, 1961) suggests that Ekman velocities of 3 to 10 cm./sec. generally toward the southeast may be expected in this coastal area during spring and fall. Although the short-term Ekman Currents, averaged on a daily basis, may be even greater, they are negligible below 200 m. They were neglected in this discussion which is concerned primarily with the main portion of the water column below 200 m.

The data from the cruises of the *Kelez* permit construction of the first geostrophic current charts off the Washington coast from a reference level of 1,500 db. Relative currents flow along contour lines of equal geopotential

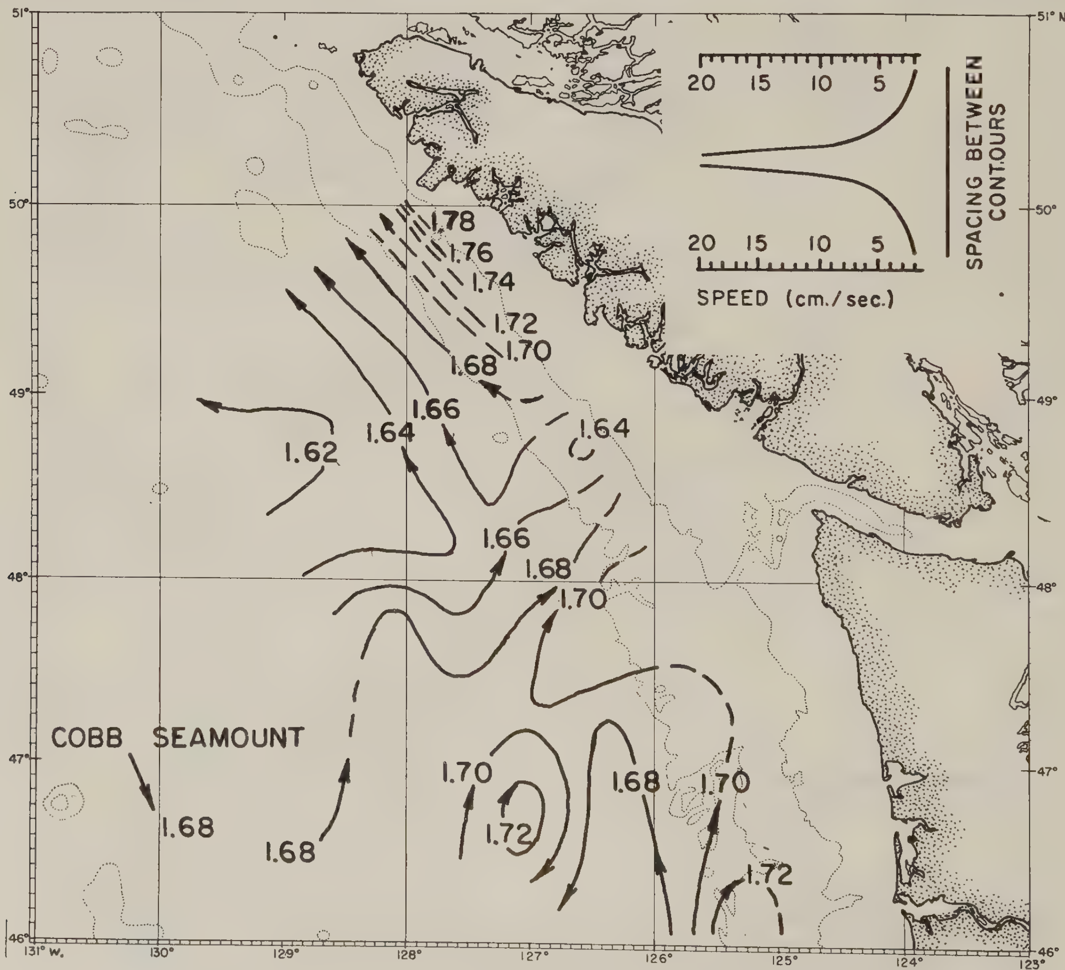
51°
51° N.
50°
49°
48°
47°
46°
131° W.
130°
129°
128°
127°
126°
125°
124°
123°
20 15 10 5
20 15 10 5
SPACING BETWEEN CONTOURS
SPEED (cm./sec.)
1.78
1.76
1.74
1.72
1.70
1.68
1.66
1.64
1.62
1.64
1.66
1.68
1.70
COBB SEAMOUNT
1.68
1.68
1.70
1.72
1.68
1.70
1.72

FIGURE 3.—Geopotential topography, 0/1,500 db., fall 1963. (The 183- and 1,829-m. depth contours are shown.)

depth with speed proportional to the gradient across them. Broken lines (figs. 2–5) represent currents in water shallower than the reference depths, which are calculated by the method used by Bennett (1959).

Surface Currents, 0 to 1,500 db.

Eddies complicated the pattern of surface geostrophic currents during the spring, but the predominant surface current within 185 km. of shore was generally toward the north (fig. 2). A major feature was the apparent divergence of onshore flow near southern Vancouver Island. North of the divergence, water from offshore veered toward the northwest and flowed generally parallel to the coast. Northwestward velocities were 10 and 12 cm./sec. at two locations on the northernmost line of stations, and a speed of 18 cm./sec. occurred off the Washington coast near lat. 47° N. The latter flow turned eastward toward shore and was not evident north of lat. 47°30′ N.

Although large eddies were also present off the coast of Washington during fall, they were absent off Vancouver Island (fig. 3). Maximum speed off the coast of Washington was 11 cm./sec. in the anticyclonic eddy near lat. 47° N., long. 127° W. The northward flow of 10 cm./sec. off the Columbia River in the vicinity of the 1,829-m. depth contour appeared to be dissipated by eddies as it proceeded north. Offshore water near lat. 48° N. flowed northeasterly toward southern Vancouver Island as it had during spring, but the distinct divergence over the continental slope was absent in the fall, and most of the water appeared to flow

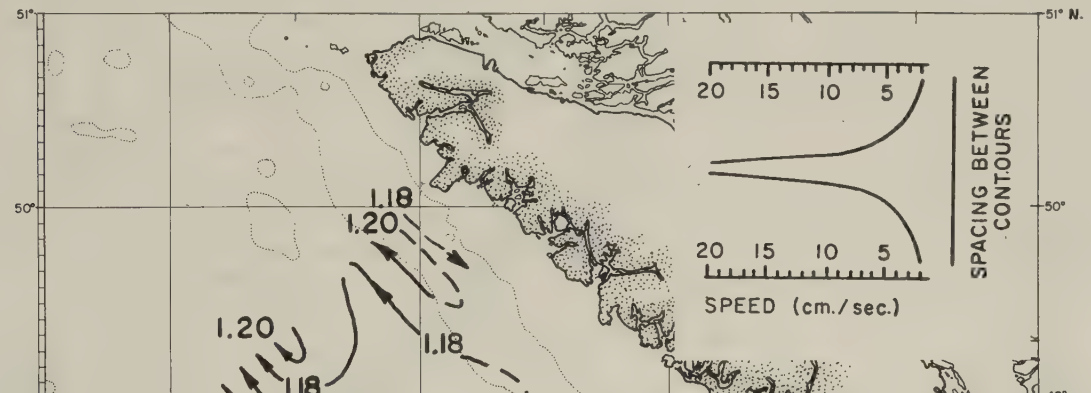

Figure 4.—Geopotential topography, 200/1,500 m., spring 1963. (The 183- and 1,829-m. depth contours are shown.)

northwesterly along the coast. A maximum speed of 20 cm./sec. occurred close to shore near Cape Cook.

Results from additional stations along the Willapa Bay line at 30-mile intervals to Cobb Seamount indicated that just east of Cobb Seamount was a weak southerly flow which suggests a meander in the general onshore movement.

In summary, the gross aspects of the surface geostrophic currents during spring and fall were similar. A major, recurring feature was the broad northeasterly movement of offshore water toward southern Vancouver Island; this flow veered northwesterly generally parallel to the coastline. Most characteristic features of the circulation off Washington were the many eddies and the apparent lack of strong northward flow of near-shore water, the Davidson Current, across lat. 48° N. Drift bottle experiments during the winter of 1965, however, indicated a significant northward flow of water over the Continental Shelf off Washington and Vancouver Island. The onshore flow which restricts the northward movement of water along the coast of Washington suggests a cause for the formation of eddies.

Lower Zone Currents, 200 to 1,500 db.

Data collected during the spring and fall of 1963 indicate the bottom of the halocline did not extend to a depth of 200 m. in the coastal area. Geostrophic currents at 200 m., therefore, represent the movement of water which possesses nearly constant properties below the halocline and is isolated from the direct in-

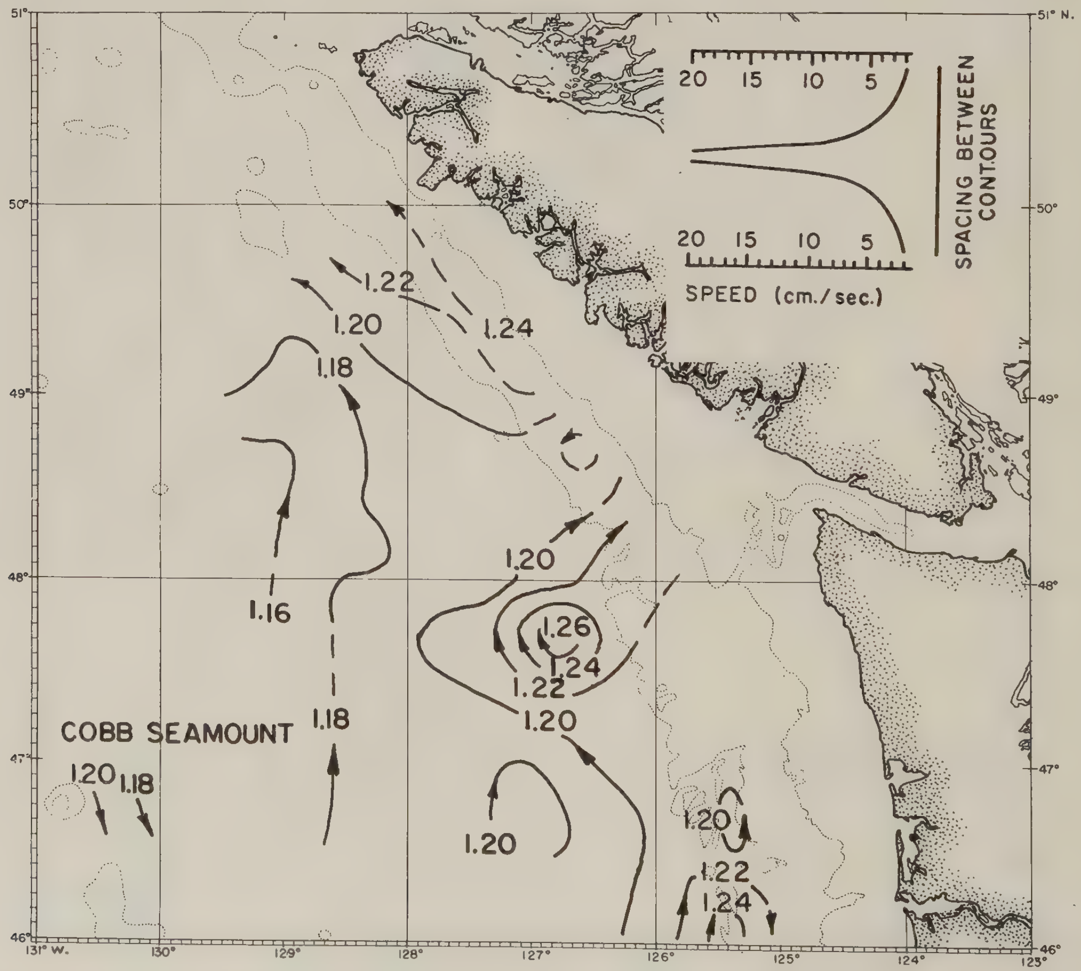
51°
51° N.
50°
49°
48°
47°
46°
131° W.
130°
129°
128°
127°
126°
125°
124°
123°
20 15 10 5
20 15 10 5
SPEED (cm./sec.)
SPACING BETWEEN CONTOURS
1.22
1.24
1.20
1.18
1.16
1.20
1.26
1.24
1.22
1.20
1.18
COBB SEAMOUNT
1.20
1.18
1.20
1.20
1.22
1.24

FIGURE 5.—Geopotential topography, 200/1,500 db., fall 1963. (The 183- and 1,829-m. depth contours are shown.)

fluence of seasonal processes (Tully and Barber, 1960). During spring the directions of geostrophic flow at 200 m. and at the surface were nearly identical (fig. 4). An exception occurred near lat. 47° N., where water on the Continental Slope veered more sharply offshore than did the surface water. The deeper flow followed the 1,829-m. (1,000-fathom) depth contour and appeared to be influenced by the local bottom topography. The maximum current of 10 cm./sec. was at 200 m., whereas the surface flow was 6 cm./sec. This condition is contrary to the characteristic decrease in speed with depth throughout most of the Subarctic Region and occurred only in this one area off the coast of Washington.

Geostrophic currents at 200 m. during fall also followed closely the direction of the surface currents (fig. 5). The speed at 200 m. was generally one-half that of the surface current north of lat. 48° N., but speeds significantly greater than the surface flow were again present off Washington. The speed of the pronounced anticyclonic eddy just south of lat. 48° N. near the 1,829-m. depth contour was 15 cm./sec., at least three times the speed at the surface.

When Dodimead et al. (1963) showed the California Undercurrent flowing northward below 200 m., the surface water flowed south, opposing the Undercurrent. Because there was no southerly surface flow during the spring and fall of 1963, this apparent reversal did not exist; but if the surface current was the slower, the Undercurrent would be evident as a relative maximum at 200 m. in the velocity profile. The vertical distribution of velocity in the upper 1,500 m. during the fall, seaward from Willapa Bay, Hoh Head, and Esperanza Inlet, showed an area within 165 to 220 km. of the Washington coast in which pronounced maxima in the velocity did occur between depths of 200 m. and 300 m. (fig. 6). The direction of flow in adjacent maxima opposed each other, apparently forming eddies. The resultant current across any line normal to the coast of Washington, although northward, was very small. Volume transport calculations indicate the magnitude of the net flow.

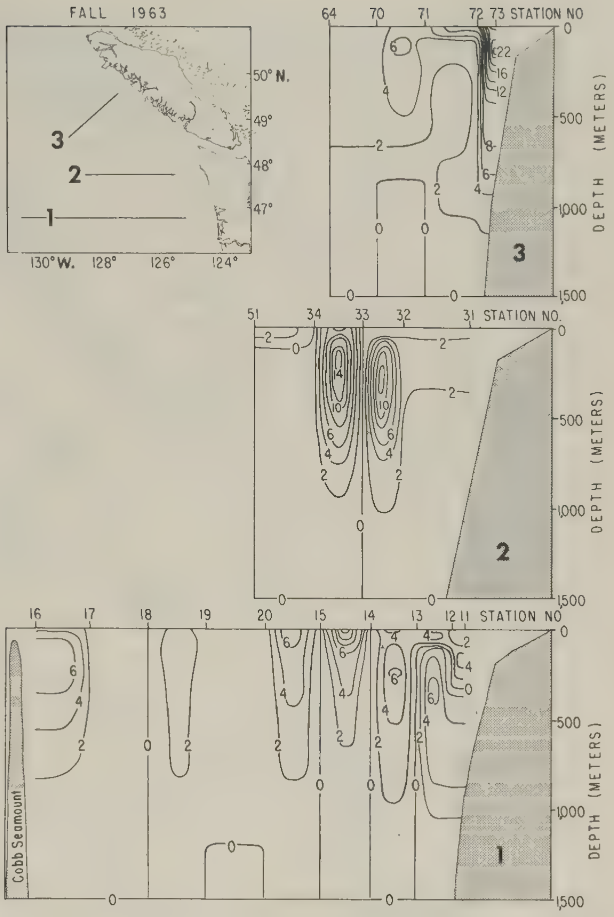

FIGURE 6.—Vertical sections of geostrophic velocity (cm./sec.) relative to 1,500 db. seaward from Willapa Bay, Hoh Head, and Esperanza Inlet, fall 1963. (Light shading indicates regions of northward flow.)

VOLUME TRANSPORT

Volume transports are calculated by integrating the geostrophic currents throughout the water column (Sverdrup et al., 1942). The volume transports indicate the resultant relative flow through the selected cross-sectional area, and are, therefore, a more reliable representation of the net flow in an area than a chart of the geostrophic currents at a particular depth. In the previous section on geostrophic currents, I pointed out that surface Ekman currents which were neglected may be in the same order of magnitude as the surface geostrophic velocities. In terms of the net transport in this coastal area during spring

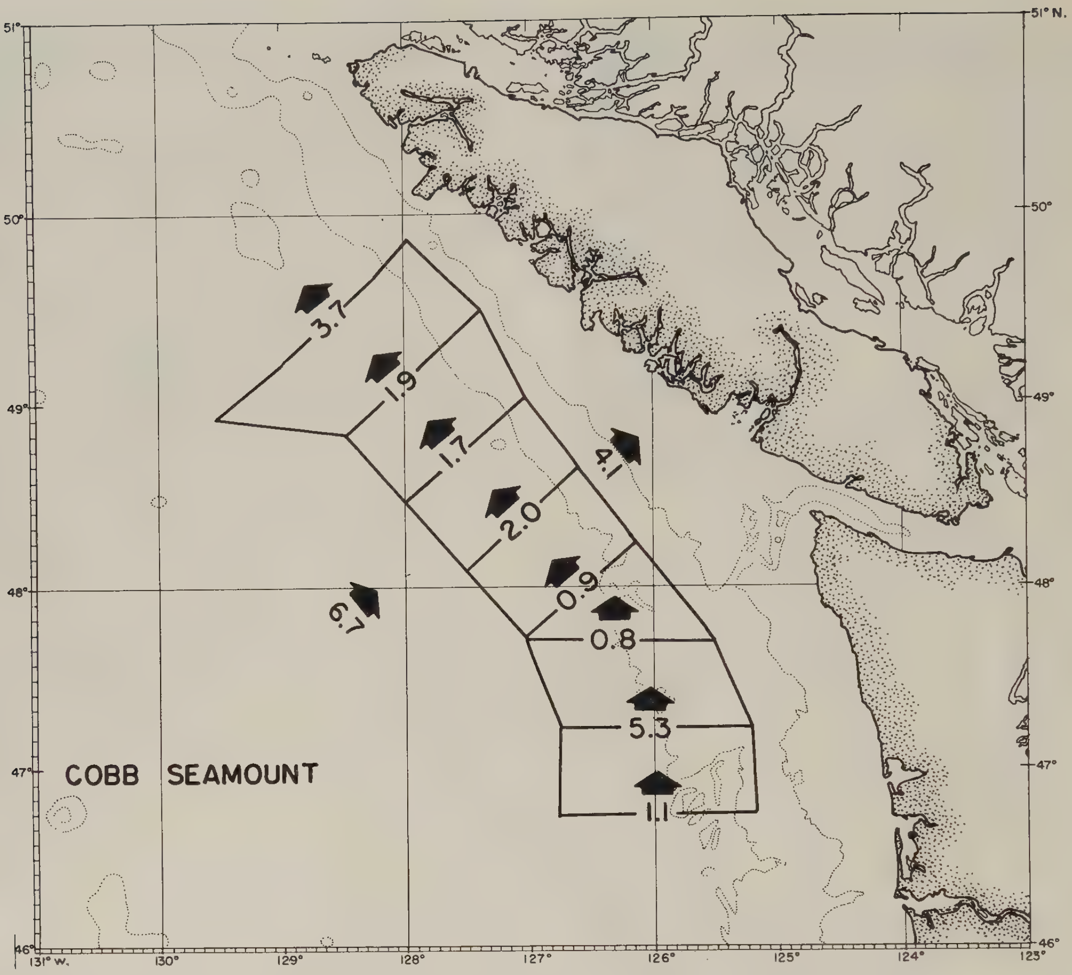

FIGURE 7.—Volume transport in 10^6m.^{3}/sec., 0 to 1,500 m., spring 1963. (The 183- and 1,829-m. depth contours are shown.)

and fall the zonal and meridional components of Ekman Transport computed by Fofonoff and Ross (1961) appear to contribute only 0.01 x 10^6m.^{3}/sec. and thus may be neglected.

During spring the net transport of water across each of the eight lines normal to the coast was directed toward the north and averaged approximately 2 x 10^6m.^{3}/sec. (fig. 7). This estimate appeared to give considerable credence to the existence of both the Davidson Current and California Undercurrent. On the other hand, the large northward flow of 5.3 x 10^6m.^{3}/sec. off the coast of Washington was part of an anticyclonic eddy; only a very weak net transport of less than 1 x 10^6m^3/sec continued northward across lat. 48° N. A relatively large volume 6.7 x 10^6m.^{3}/sec. entered the area from offshore, of which 4.1 x 10^6m.^{3}/sec. apparently flowed onshore across the Continental Slope where calculation of volume transport to 1,500 m. is less meaningful. The net northward transport increased to 3.7 x 10^6 m.^{3}/sec. across the northernmost line and had the same direction and magnitude as that reported by Bennett (1959) during August 1955 for the near-shore area between lat. 50° and 55° N., just north of this study area.

During fall the greatest northward transport again occurred off the northern coast of Vancouver Island; no significant change appeared in the volume of water flowing northward past Cape Cook (fig. 8). Off the Washington coast the net transport was again about 1 x 10^6m.^{3}/sec., but the direction reversed across succes-

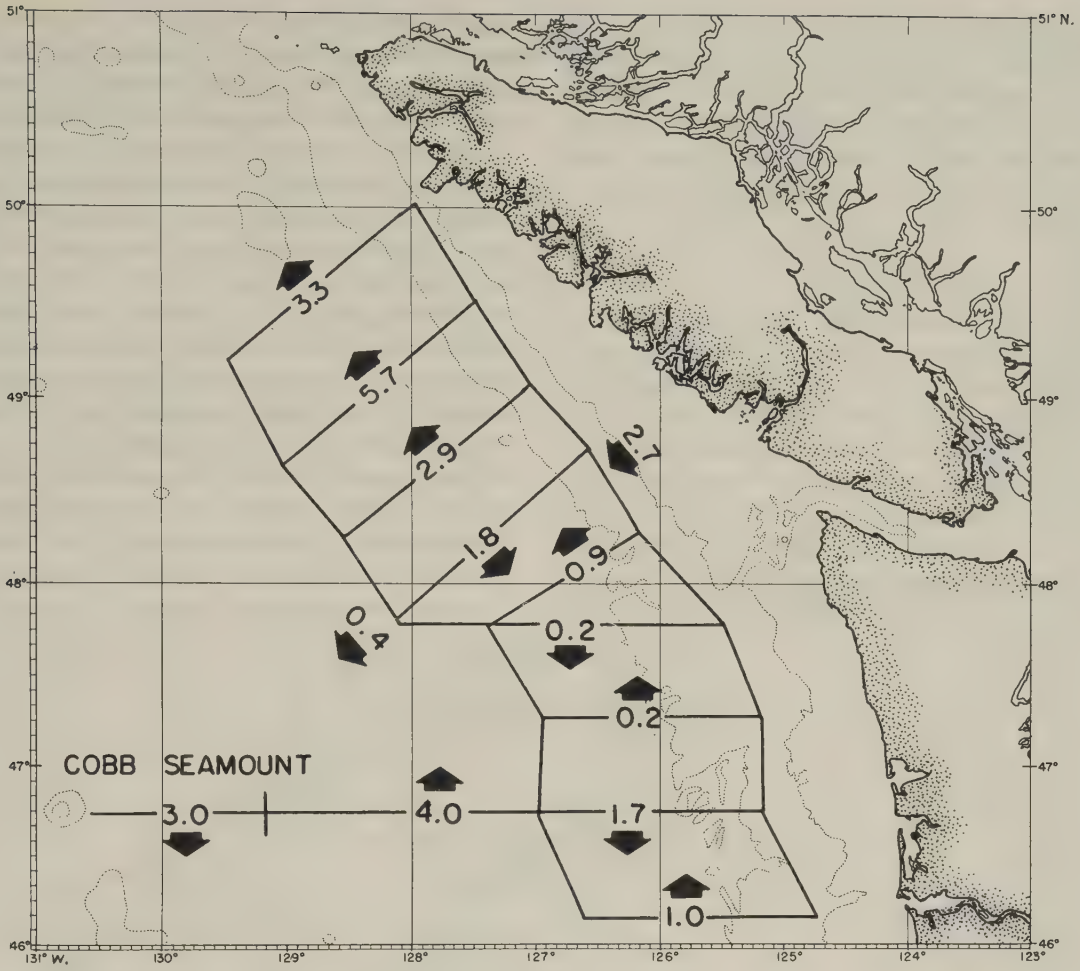

FIGURE 8.—Volume transport in 10^6m.^{3}/sec., 0 to 1,500 db., fall 1963. (The 183- and 1,829-m. depth contours are shown.)

sive lines normal to shore. The onshore movement evident during spring had reversed to 0.4 x 10^6m.^{3}/sec. in the offshore part of the area and 2.7 x 10^6m.^{3}/sec. Seaward across the Continental Slope. The net transport across the line from Willapa Bay to Cobb Seamount was less than 1 x 10^6m.^{3}/sec. Compared with a transport of 14 x 10^6m.^{3}/sec. for the Gulf of Alaska (Bennett, 1959), these results indicate a lack of significant net transport along the coast of Washington within 500 km. of shore.

The surface Davidson Current and the subsurface California Undercurrent reported by previous authors, therefore, did not contribute more than 1 x 10^6m.^{3}/sec. to the net northward transport of water along the coast of Washington. Although the total volume of transport was the same in spring and fall, an increase in the California Undercurrent was implied by the distribution of properties at and below 200 m. south of lat. 48° N.

DISTRIBUTION OF PROPERTIES

Although the most common method of determining oceanic circulation is the calculation of geostrophic currents and transports from observed values of temperature and salinity at standard depths, deductions concerning flow can also be made directly from the observed distributions of these water properties. Reasonable confidence may be placed in the interpretation of the circulation, particularly when the direction of flow suggested from the distribution of properties supports the calculated geostrophic currents. The following items are discussed: features of the distributions of salinity, temperature, and dissolved oxygen; changes in these properties near the bottom along the continental terrace; and water mass movements implied by temperature-salinity relationships.

SALINITY

Throughout most of the Subarctic Region, the salinity structure consists of three distinct permanent zones: (1) an isohaline upper zone, which extends from the surface to about 100 m.; (2) a halocline, in which the salinity increases about 1‰ between 100 and 200 m.; and (3) a lower zone, in which the salinity gradually increases with depth. The mechanism for the maintenance of this structure was discussed by Dodimead et al. (1963).

Perhaps the most striking changes in the distribution of properties within the coastal areas occur in the salinity distribution in the upper zone and are due to the intrusions of fresh-water runoff from coastal rivers. Various authors have attempted to distinguish oceanic and coastal water on the basis of the salinity distribution near the surface. In the North Pacific Ocean, Doe (1955) used the 32.5‰ isohaline as the boundary between offshore and coastal water masses in the upper zone; Dodimead et al. (1963) defined the extent of a coastal domain by the 32.4‰ isohaline; and Budinger et al. (1964) suggested the Columbia River effluent could be traced by salinities less than 32.5‰. Good agreement has thus been reached concerning a definable boundary be-

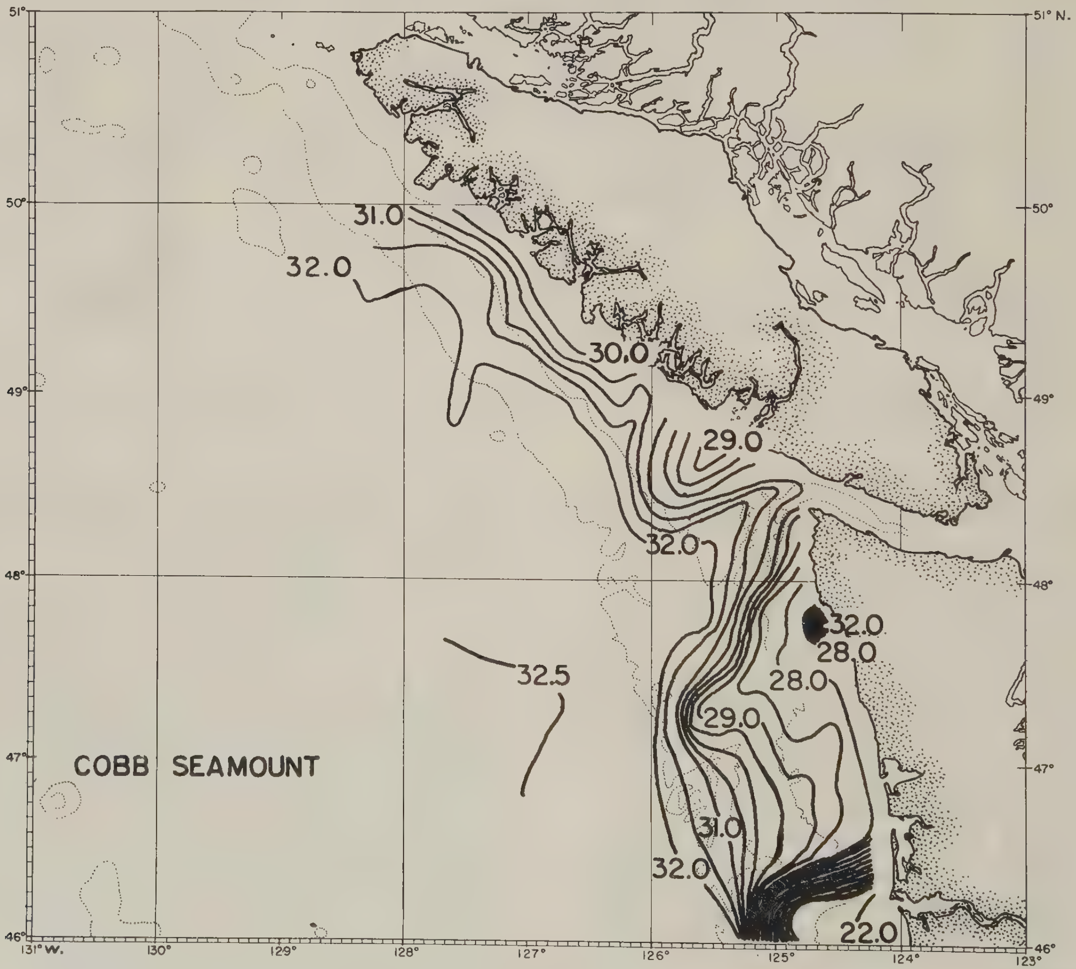

FIGURE 9.—Surface salinity (‰), spring 1963. (The 183- and 1,829-m. depth contours are shown.)

tween oceanic and coastal water, and the effects of dilution have been shown to extend over several hundred kilometers from shore (Favorite, 1961). Sharp gradients, or fronts, found closer to shore, however, are more interesting and much more complex.

The distribution of surface salinity during spring showed that the 32.5‰ isohaline approached within 160 km. of shore off the coast of Washington, but the most significant feature was the front associated with the 32.0‰ isohaline (fig. 9). The controversy regarding the precise definition of the term front in oceanographic usage has been discussed by Griffiths (1965). Front is used here in the sense that Cromwell and Reid (1956) defined the term, ". . . a band along the sea surface across which the density changes abruptly." The change of surface temperature near the front was not appreciable compared with the salinity change; thus the density change at the front was dominated by the relatively sharp decrease in surface salinity. Although no particular isohaline appeared to define the exact extent of the front throughout the area, gross changes in the position of the front may be seen by tracing the extent of the 32.0‰ isohaline. The largest gradient of surface salinity was about 80 km. from shore near lat. 46° N. where the front was apparently being maintained by effluent less was 22‰ from the Columbia River. The maximum seaward extent of the 32.0‰ isohaline was 112 km. near lat. 47° N.; at lat. 48° N. it had decreased to 64 km., and all along the coast of Vancouver Island it was confined to within 48 km. of shore. It is not clear whether the large tongue of dilute water off the central coast of Washington was a remnant of water from the Columbia River which had proceeded north along the coast during the winter or if it came directly from the Strait of Juan de Fuca. A patch of relatively high salinity water (> 32.2‰) about 11 km. seaward of Hoh Head indicated an area of local upwelling.

A vertical section of salinity extending seaward from Willapa Bay illustrates the major changes in salinity with depth and distance from shore during spring (fig. 10). Dilute water of less than 32.0‰ in which the isolines were closely spaced, appeared to protrude seaward in the form of a tongue. Although the 32.0‰ isohaline that occurred at the leading edge of this tongue underwent large fluctuations in its seaward extent along the coast, the nearly constant depth of the 32.0‰ isohaline near shore shows that the

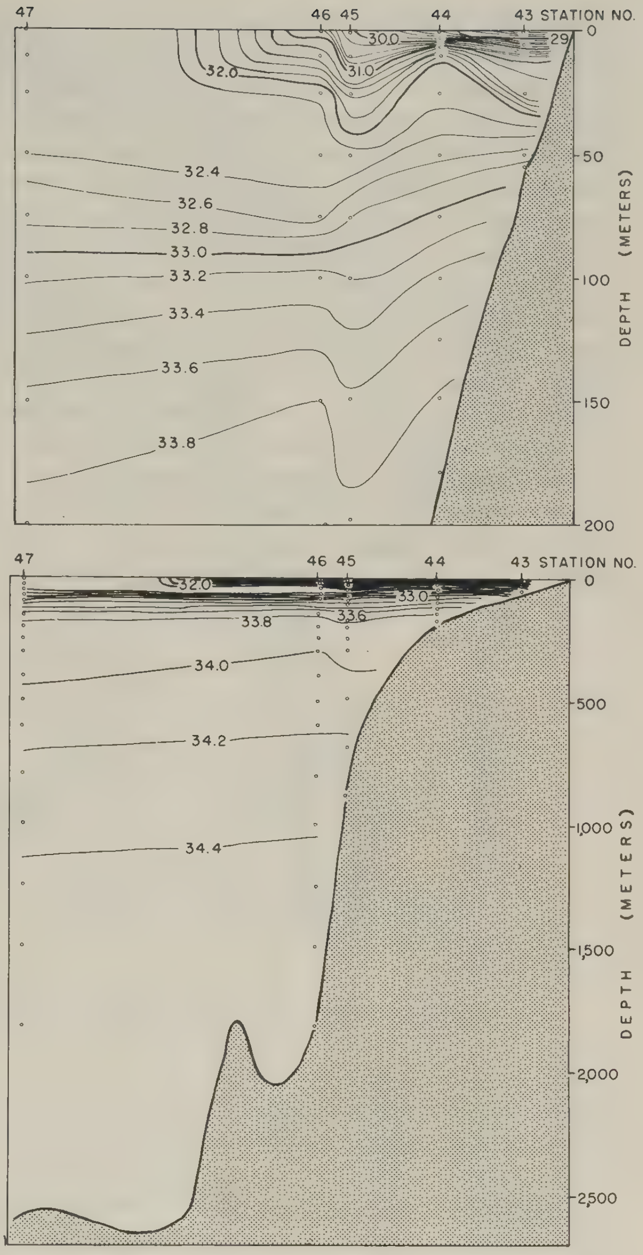

FIGURE 10.—Vertical sections of salinity (‰), 0 to 200 m. and 0 to 2,500 m., along Willapa Bay line, spring 1963.

major effect of the dilution off the coast of Washington was limited to the upper 30 to 40 m. Offshore, the three vertical zones characteristic of the Subarctic Region were present; although the boundaries between zones generally rose toward shore, the halocline and lower zone could be traced continuously inshore until they ended at the continental terrace.

Tully and Barber (1960) suggested that across the boundary of the halocline-lower zone 33.8 ± 0.1‰, only upward transfer of water existed; thus the depth of this surface forms the ultimate limit of downward transfer of water from the surface. Changes in properties below this surface are, therefore, primarily due to advection, not directly influenced by seasonal changes near the surface. The 33.8‰ surface was about 170 m. deep offshore but rose to about 130 m. near the 183-m. depth contour.

A horizontal section of salinity at 200 m. during spring showed uniform values of salinity just below the halocline; the range was from about 33.86‰ to 33.93‰ (fig. 11)—a marked contrast to the range of surface salinity, 22.0‰ to 32.5‰. A second important feature was the tongue of relatively high salinity (> 33.92‰) which appeared to point northward near the 1,829-m. depth contour off Willapa Bay. Although many of the features in the coastal area during the fall were similar to those during the preceding spring, important changes occurred near the surface between spring and fall. The salinity front was consistently nearer shore, 48 km. to 64 km. (fig. 12). The tongue of dilute water

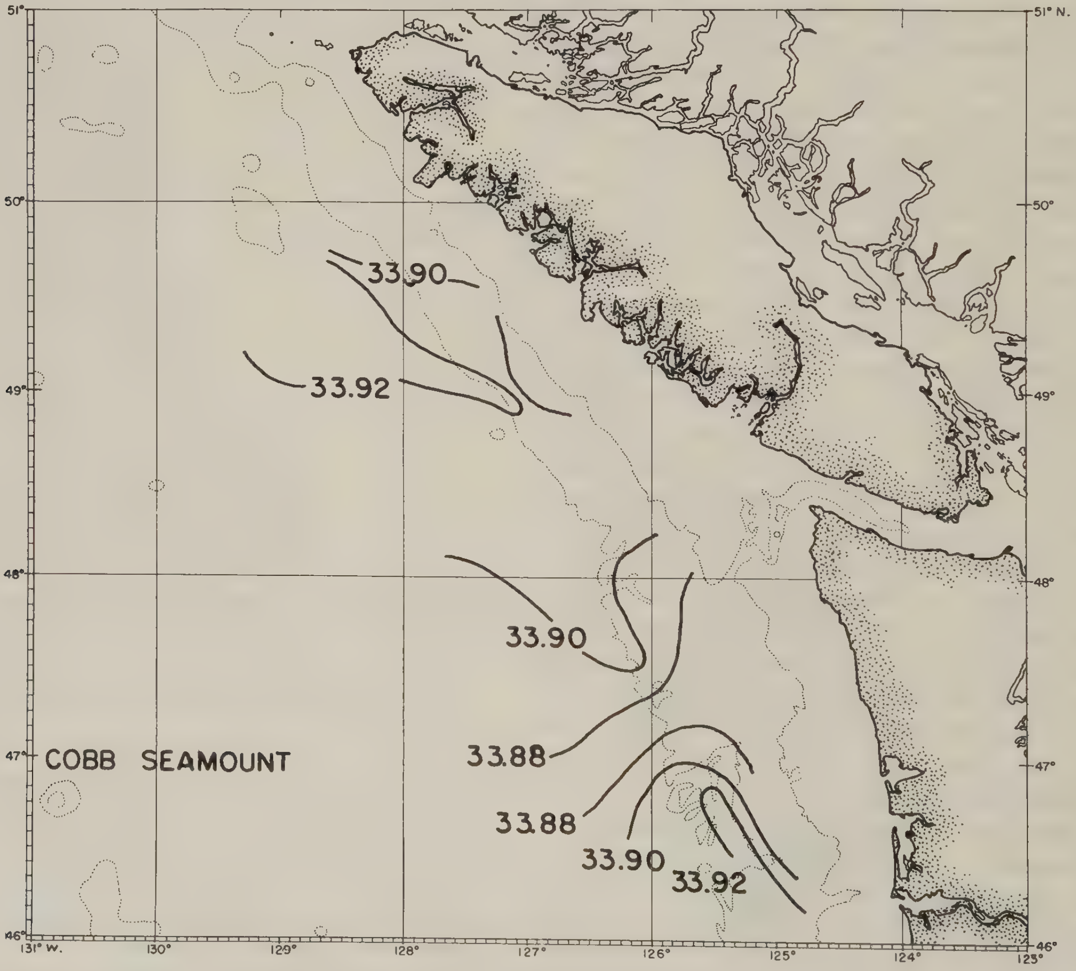

FIGURE 11.—Salinity (‰) at 200 m., spring 1963. (The 183- and 1,829-m. depth contours are shown.)

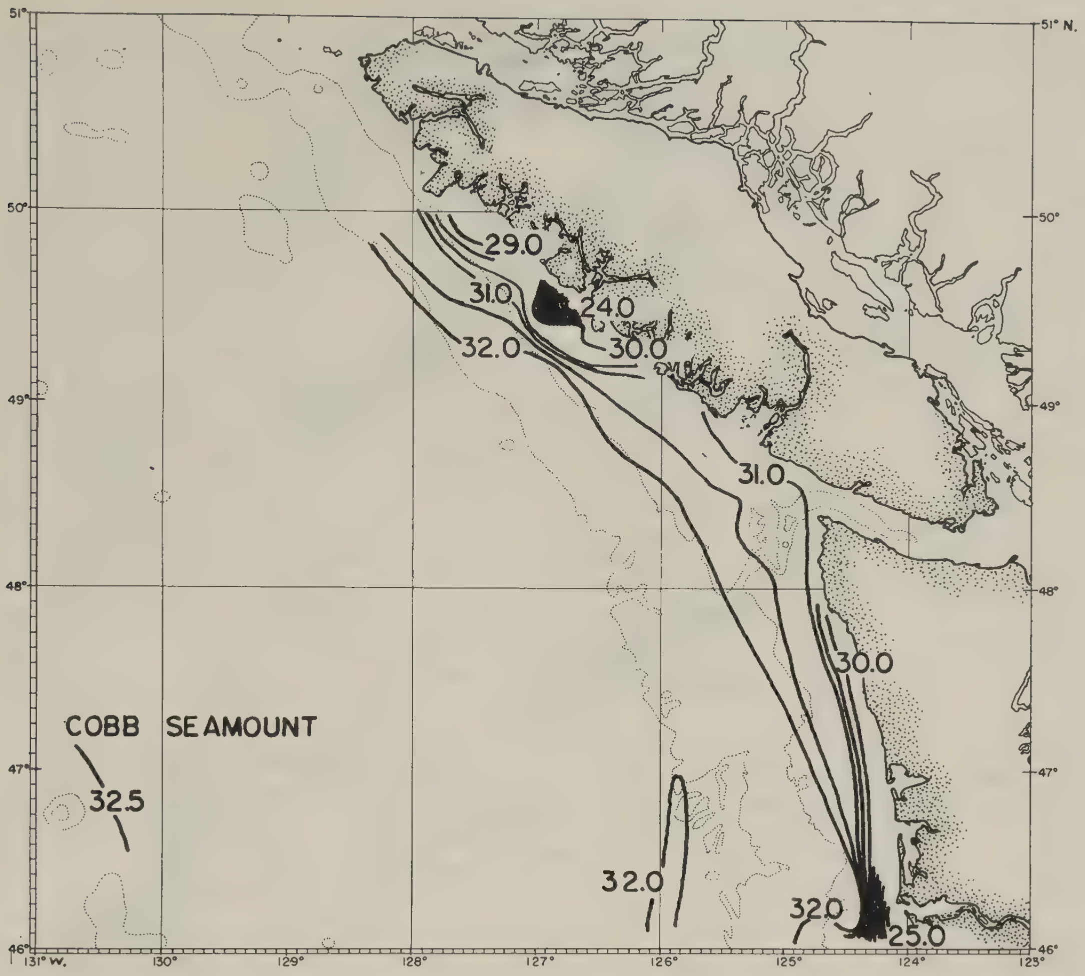

FIGURE 12.–Surface salinity (‰), fall 1963. (The 183- and 1,829-m. depth contours are shown.)

which had protruded twice as far seaward from the coast of Washington during the spring was absent in the fall. The 32.5‰ isohaline had shifted seaward from 160 km. to 400 km. by fall. Although the boundary between the halocline and lower zone fluctuated over a greater depth range during the fall, the major structural zones were again present and continuously defined along each section normal to shore. At 200 m. the maximum salinity increased to 33.96‰ between Willapa Bay and lat. 48° N. (fig. 13). The small tongue of greater salinity present during spring had enlarged to form a continuous ridge of high salinity along the coast with an axis about 140 km. from shore. This feature was more complex north of lat. 48° N. where the salinity decreased.

TEMPERATURE

In the Subarctic Pacific Region the water above the halocline begins to receive a net gain in heat in April and continues to warm into September (Dodimead et al., 1963). During the spring the surface-temperature gradient along the coast was uniform; temperatures from Vancouver Island to the Columbia River increased from 9.0° C. to 13.5° C. (fig. 14). Off the coast of Vancouver Island the surface isotherms were generally oriented northeast-southwest, normal to the shore, and showed no apparent relation to the surface-salinity front. Off the coast of Washington, however, the isotherms generally ran from north to south, parallel to shore. Their configuration agreed closely with the surface isohalines.

Vertical sections of temperature during

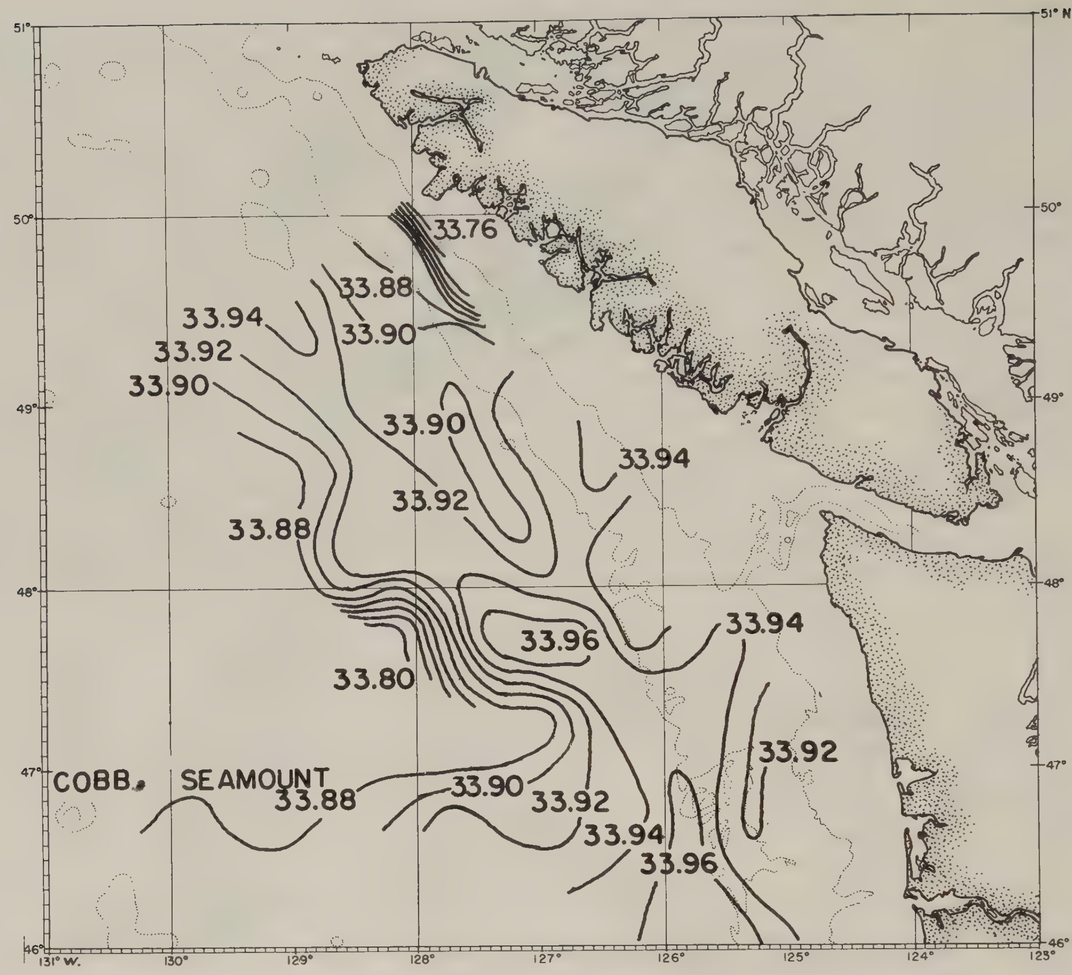

FIGURE 13.—Salinity (‰) at 200 m., fall 1963. (The 183- and 1,829-m. depth contours are shown.)

spring, one seaward from Cape Cook and the other seaward from Willapa Bay, illustrate the changes in temperature with depth and distance from shore as well as difference in temperature along the coast between the northern and southern parts of the area (fig. 15).

Characteristically the decrease of temperature with depth throughout the water column was inconsistent only within the halocline which contained sporadic inversions not in excess of 0.5° C. Below the halocline the temperature decreased logarithmically toward the bottom.

As was true with salinity, the most pronounced changes within the area took place in the upper layers. The dilute water near shore had a weak vertical gradient. Offshore from Cape Cook the upper 50 m. was isothermal, but toward the south, the magnitude of the seasonal thermocline increased between the surface and 30 m. Within the halocline off the Washington coast the isotherms rose toward shore over the Continental Shelf, but beyond the shelf they sloped slightly downward toward shore. The temperature increase from Cape Cook to Willapa Bay extended to a depth of at least 200 m. In the lower zone, the isotherms were relatively level. Although the variations of temperature at a particular depth below the halocline were small, the temperature distribution at 200 m. did show an unusual feature. A tongue of cold water (<6.8° C.) extended shoreward near the middle of Vancouver Island, interrupting a band of warmer water

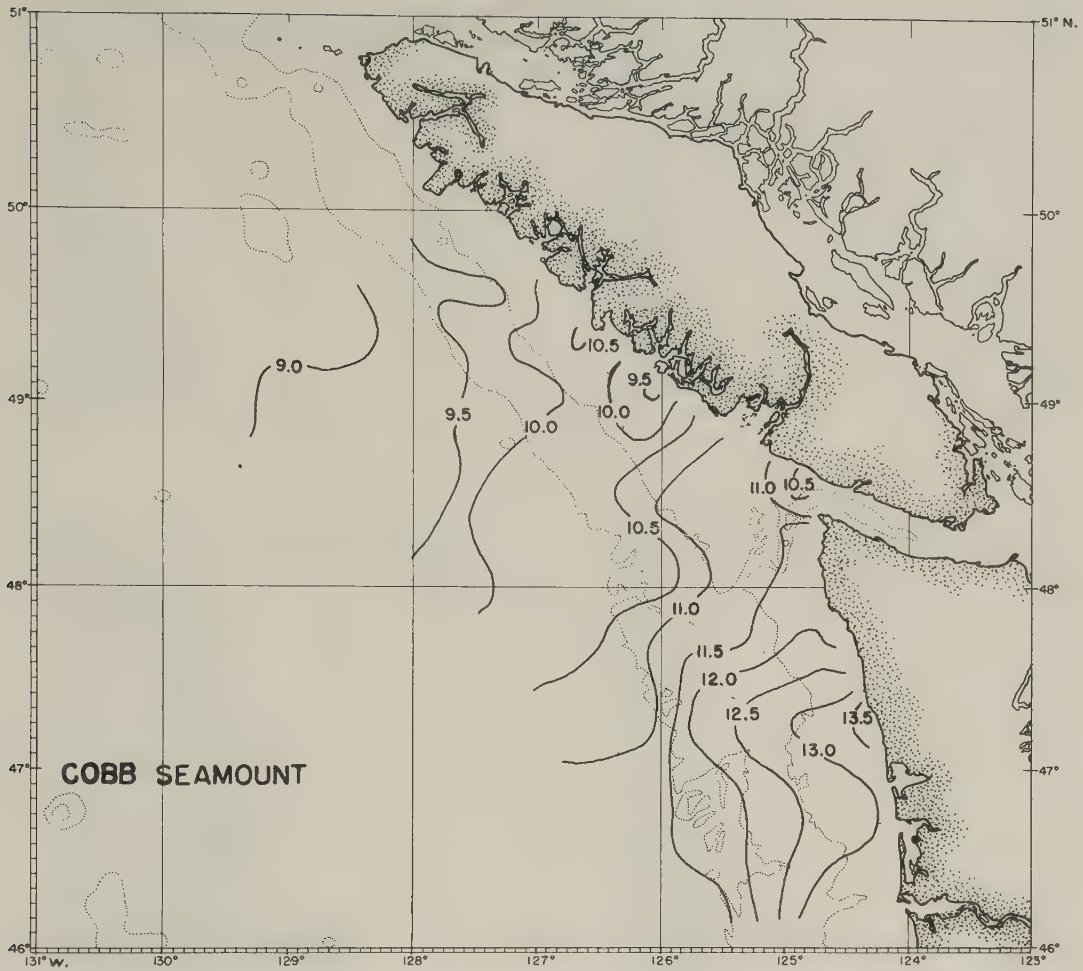

FIGURE 14.—Surface temperature (°C.), spring 1963. (The 183- and 1,829-m. depth contours are shown.)

(>7.2° C.) near the 1,829-m. depth contour (fig. 16).

Differences between temperatures during spring and fall were most pronounced above the halocline, in the zone affected by seasonal heating. Significant changes also occurred, however, within the lower zone which is not influenced directly by the seasonal heating; changes in circulation are implied.

Although the gradient of the surface temperature between northern Vancouver Island and the Columbia River was the same during each season, temperatures were generally 1.0° C. higher at each location during the fall (fig. 17). The most pronounced changes were near shore. During spring, warming was appreciable only near the surface in the dilute water off the coast of Washington, but in the fall the water was distinctly warmer over the entire Continental Shelf than offshore. The resulting temperature distribution shows a tongue of warm water extending northward along the coast and the maximum temperature along any line normal to shore near the edge of the Continental Shelf.

Comparison of fall and spring conditions along the same two vertical sections indicated many differences and similarities with depth and distance from shore. The most pronounced differences were in the upper 70 m. In contrast to the gradual decrease of temperature seaward during spring was the presence of two maxima during the fall—one at the surface near the edge of the Continental Shelf and the

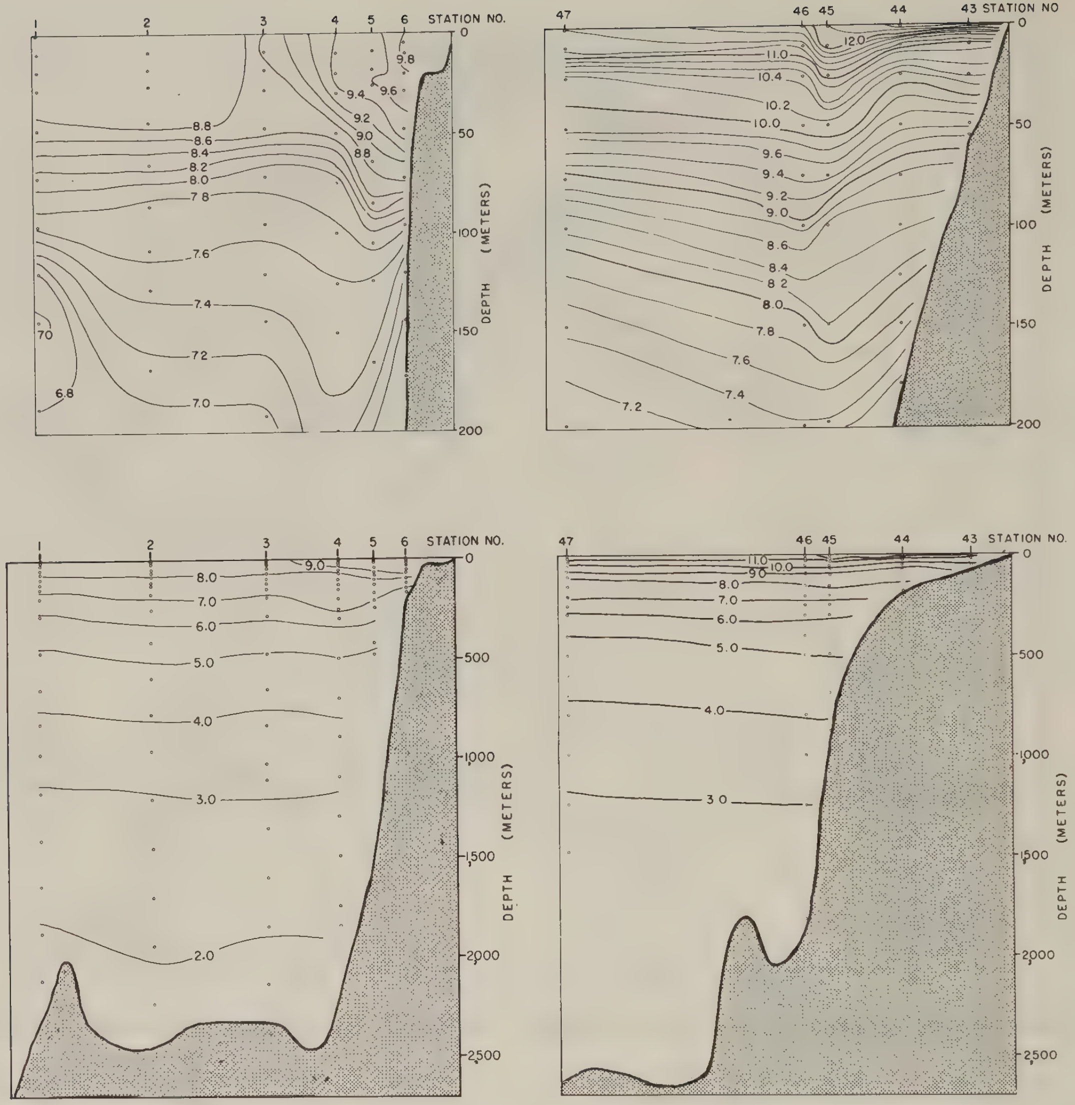

FIGURE 15.—Vertical sections of temperature (°C.), 0 to 200 m. and 0 to 2,500 m., along Cape Cook and Willapa Bay lines, spring 1963.

other at depth between 20 and 50 m. near shore. Apparently both maxima resulted from surface cooling and vertical mixing which had affected only the dilute water in the upper 20 m. Seaward of the salinity front, the upper 50 m. of the water column was isothermal off Cape Cook during both seasons. Southward of Cape Cook the magnitude of the thermocline again increased but by fall had deepened from the range 0 to 30 m. to between 50 and 70 m. in the top of the halocline. Temperature inversions were more frequent in the fall within the halocline, and the near-shore isotherms showed a slight depression or convergence. Vertical sections normal to shore during fall as in the spring showed the logarithmic decrease of temperature with depth and the level isotherms in the lower zone extending seaward from the Continental Slope.

Despite this general uniformity in temperature structure, minor changes did occur in the temperature distribution at 200 m. (fig. 18). The tongue of warmer water (> 7.2° C.) noted during spring changed: it became continuous along the coast, occupied a much larger area, and had a greater maximum temperature dur-

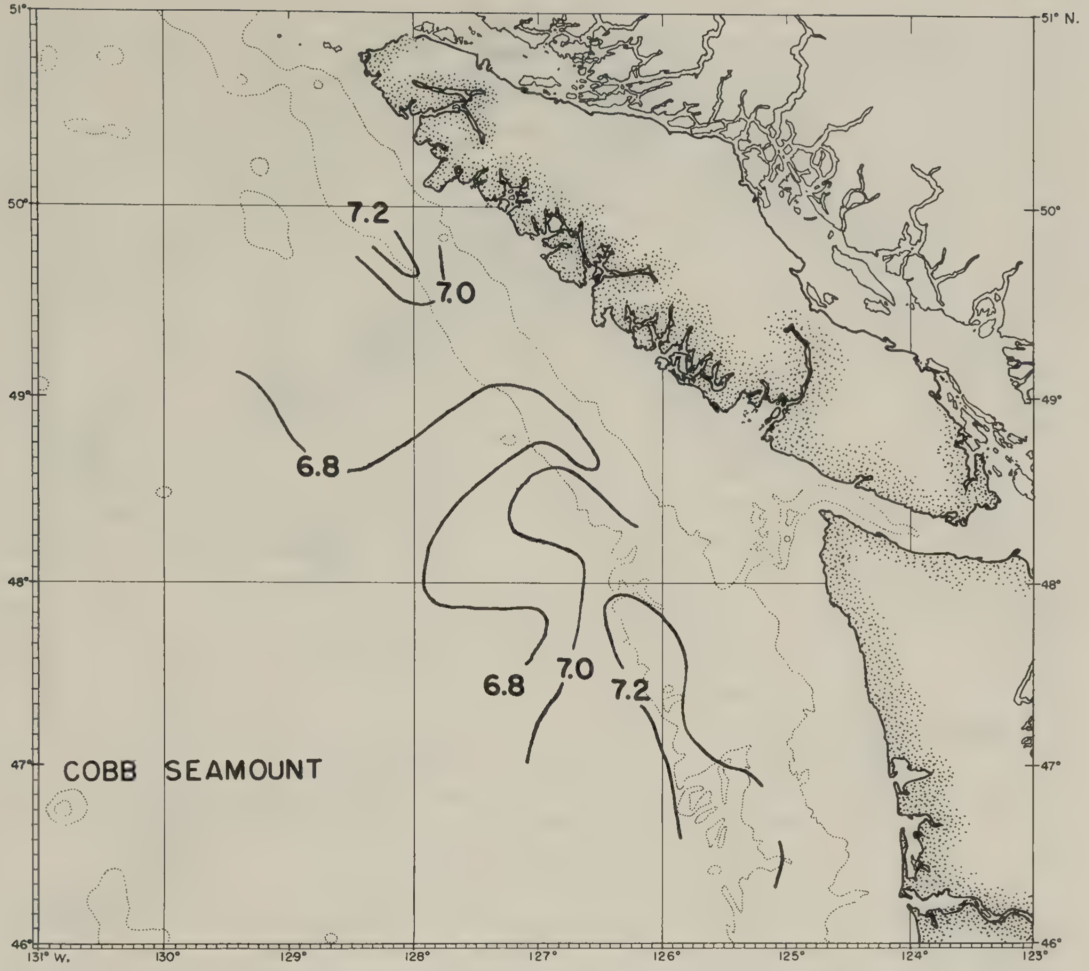

FIGURE 16.—Temperature (°C.) at 200 m., spring 1963. (The 183- and 1,829-m. depth contours are shown.)

ing fall—7.6° C. Although this increase in temperature between spring and fall was slight, it may be significant compared with the small range of values at 200 m. The association of the warm water near the coast of northern Vancouver Island with the lowest salinity values implied a local convergence. Offshore the cold water was also of low salinity. The warm water off the coast of Washington near the 1,829-m. depth contour, however, was associated with the high-salinity ridge; a significant change in water mass is indicated.

DISSOLVED OXYGEN

The distribution of dissolved oxygen during the spring was obtained only over the continental terrace between the depths of 55 m. and 1,829 m. As with the distributions of temperature and salinity, the sharpest vertical gradient occurred within the halocline. Below the saturated or mixed layer, about 50 m. deep, values decreased sharply to about 300 m. Below 300 m., concentrations decreased gradually to a minimum near 900 m., below which values gradually increased toward the bottom.

Samples obtained at each station during the fall permit comparison of conditions near shore and offshore. The vertical section off Willapa Bay shows the complex distribution of dissolved oxygen in the upper 300 m. (fig. 19). Deeper isolines were relatively level and the oxygen minimum near 900 m. extended offshore without significant change in depth. The isolines within the upper 300 m. usually fol-

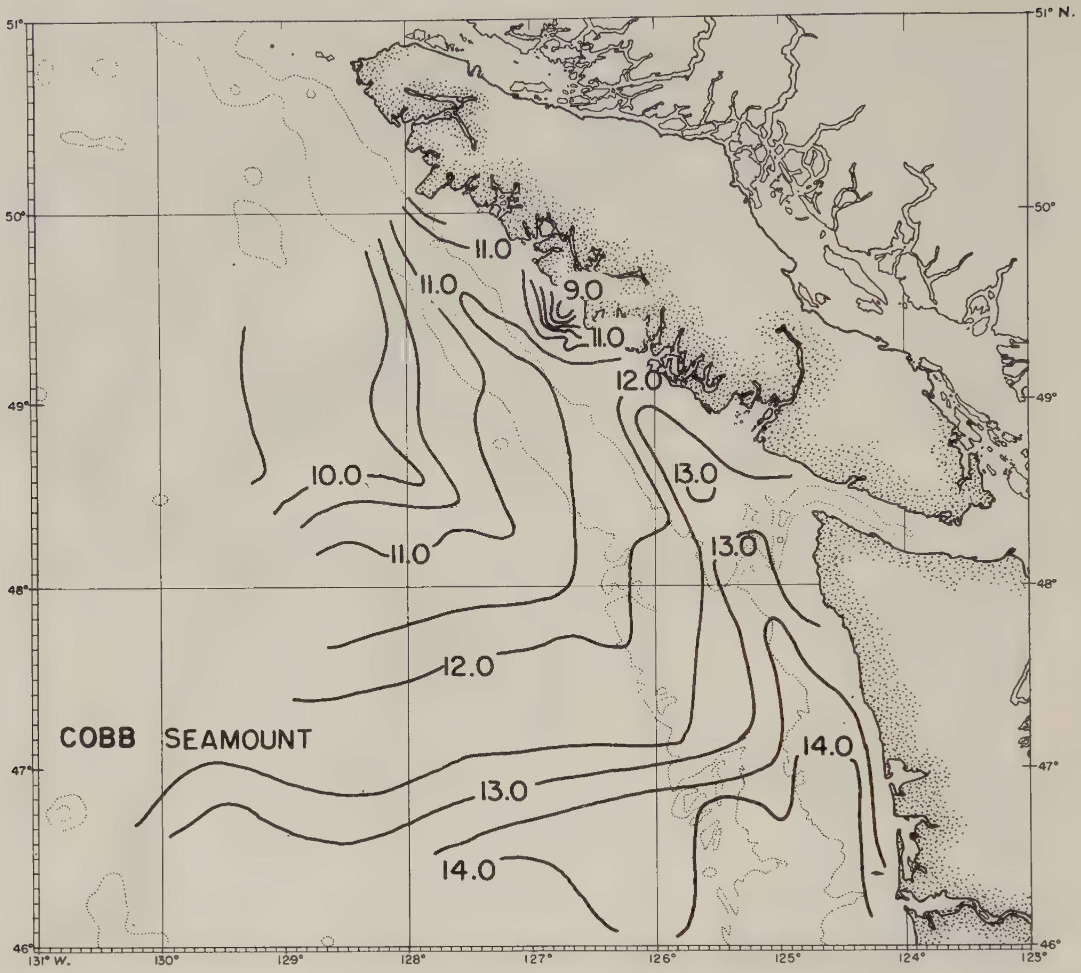

FIGURE 17.—Surface temperature (°C.), fall 1963. (The 183- and 1,829-m. depth contours are shown.)

lowed the configuration of the isohalines or isotherms, but were inclined generally upward toward shore. The rise reflected lower oxygen values near shore during spring and fall; minor inversions of dissolved oxygen were more frequent during fall, just below the bottom of the halocline near 200 m. A plot of dissolved oxygen at 200 m. during the fall (fig. 20) showed that this band of low oxygen concentration (< .20 mg. at./l.) was continuous along the entire coast over the Continental Slope and closely followed the high-salinity ridge (fig. 13).

Comparison of fall conditions with those over the Continental Slope during the preceding spring indicated that oxygen values at 200 m. had decreased on the average, by about 0.05 mg.at./l. If we assume that the seasonal change in biological utilization of dissolved oxygen was negligible, this decrease in dissolved oxygen concentration corroborates the change in water-mass characteristics between spring and fall previously indicated by the increase in temperature and salinity at 200 m. off the coast of Washington.

CONDITIONS NEAR THE BOTTOM

To determine changes in salinity, temperature, and dissolved-oxygen concentrations at a particular depth close to the sea floor along the continental terrace, samples were obtained as near the bottom as feasible—55 m., 183 m., 914 m., and 1,829 m. along each of the nine lines normal to shore. At the 55-m. and 183-m. sta-

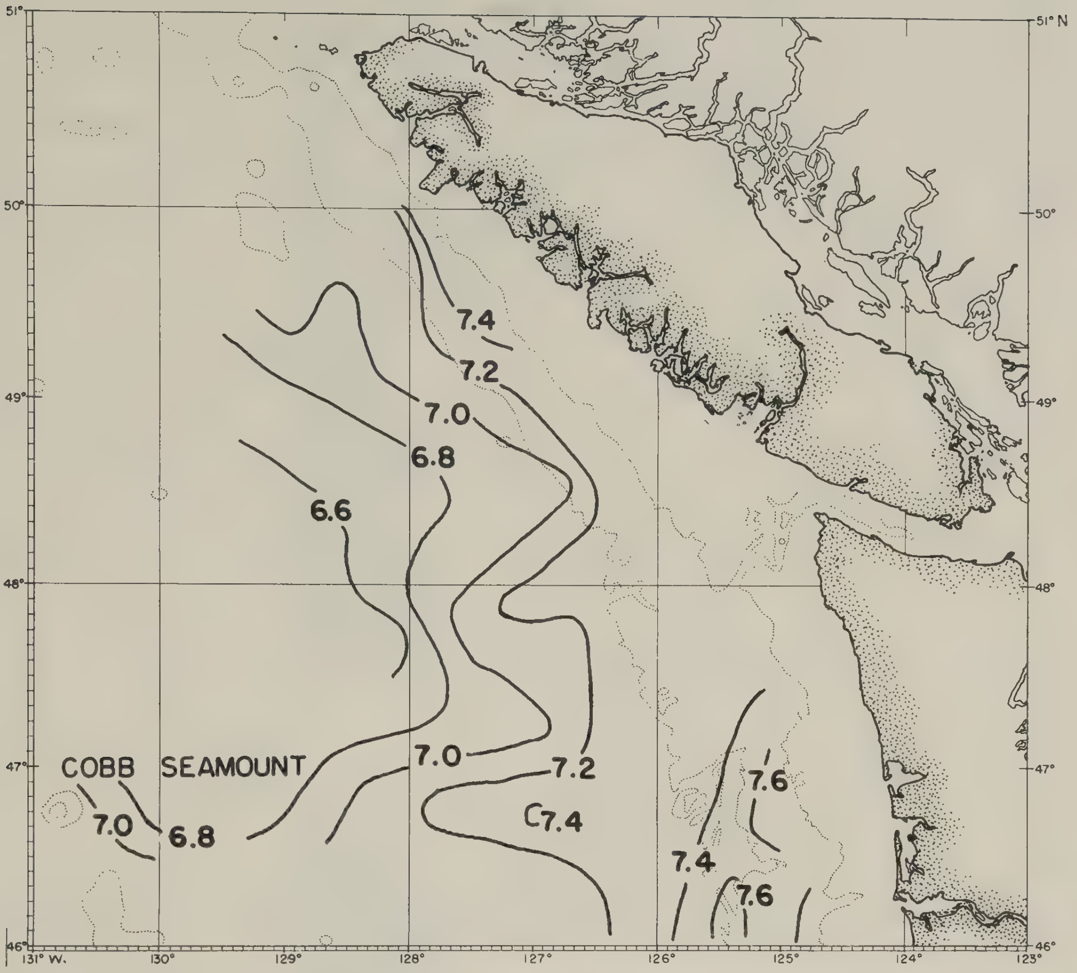

FIGURE 18.—Temperature (°C.), at 200 m., fall 1963. (The 183- and 1,829-m. depth contours are shown.)

tions, Nansen bottles were tripped 5 m. from the bottom by two methods. In the first method, the Nansen bottle is placed 5 m. above a weight suspended on the end of the wire, and the bottle is tripped by a messenger when a change in wire tension indicates the weight is striking the bottom. In the second method, a Nansen bottle attached to a tripping mechanism is reversed when a weight suspended 5 m. below the device strikes the bottom. Although agreement of results from both methods was good, values obtained by the first method were used for most stations. Because of the limited depth range of the vessel's echo sounder (about 550 m.) and the inability to detect the bottom by wire tension at great depths, the locations of the 914-m. and 1,829-m. stations were determined from charted depths; thus, the interval between the deepest bottle and the bottom depended upon the accuracy of the charted soundings and the vessel's position.

The spring values of salinity and temperature near the bottom varied most at shallow depths along the Continental Shelf and were uniform along the Continental Slope (fig. 21). At 55 m. salinity values were uniform between 31.9‰ and 32.0‰ north of the Strait of Juan de Fuca, but increased off Washington. The maximum of 33.4‰ was near the mouth of the Columbia River. The range of temperature values at 55 m. was about 1.0° C. The minimum value occurred off the Columbia River. The maximum salinity and minimum temperature indicated that water which is

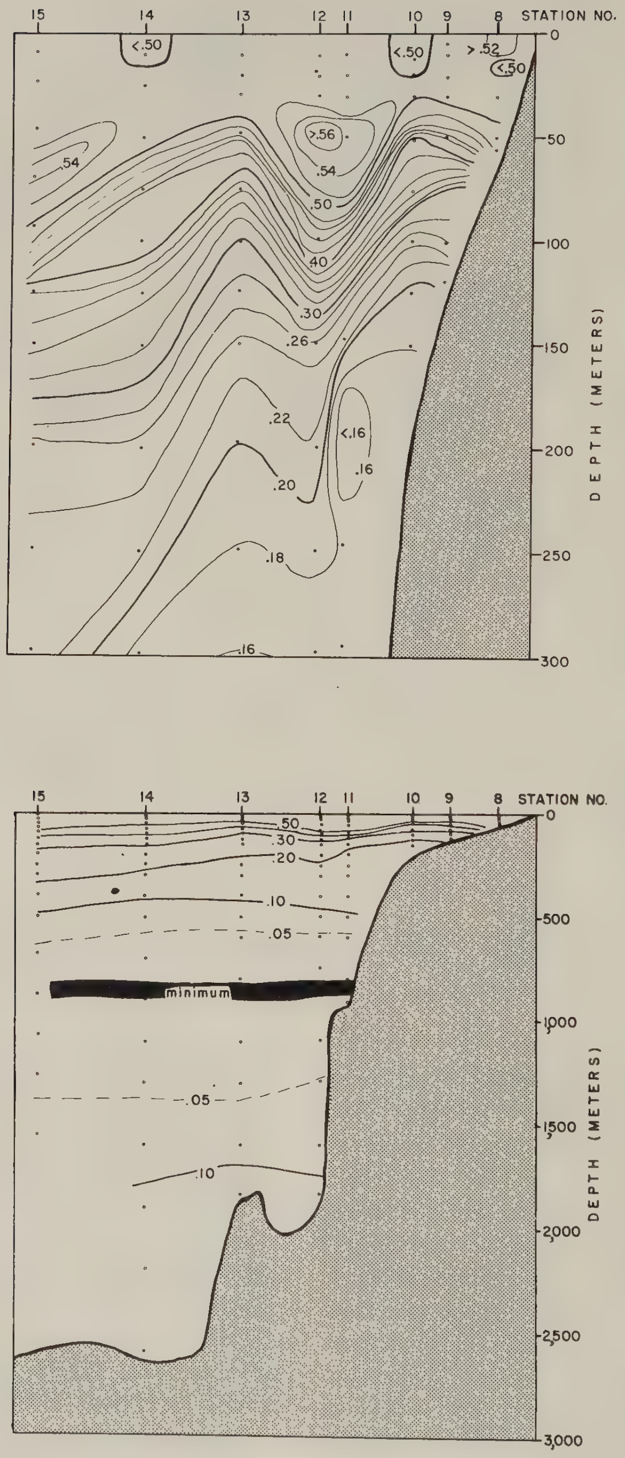

Figure 19.—Vertical sections of dissolved oxygen (mg.at./l.), 0 to 300 m. and 0 to 3,000 m., along Willapa Bay line, fall 1963.

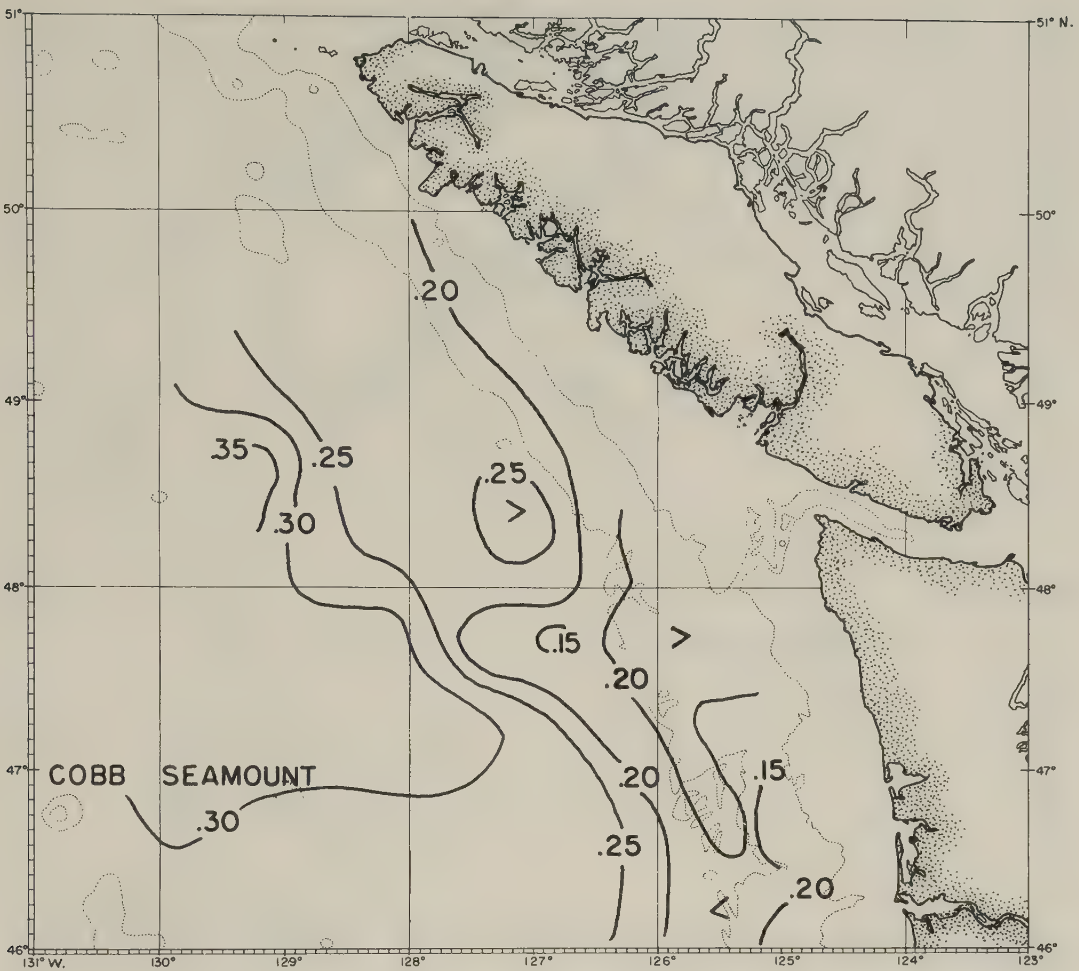

FIGURE 20—Dissolved oxygen (mg.at./l.) at 200 m., fall 1963. (The 183- and 1,829-m. depth contours are shown.)

normally found at a greater depth had moved shoreward in this area. Conditions near the bottom were reversed from those at the surface where the salinity was at a minimum and the temperature was at a maximum. At 183 m. the range of salinity was much smaller—between 33.67‰ and 33.95‰ — but the range of temperature at 183 and 55 m. was the same, 1.0° C. The salinity did not vary significantly along the coast and temperatures increased only slightly toward the south—about 0.1° C. Upwelling, therefore, was not taking place at 183 m. The range of values continued to decrease with depth. Changes in salinity ranged from 0.08‰ at 914 m. to 0.07‰ at 1,829 m., and differences in temperature ranged from 0.15° C. at 914 m. to 0.10° C. at 1,829 m. These minor variations indicated no significant change in salinity or temperature near the bottom along the Continental Slope during spring between the Columbia River and Cape Cook.

Values of dissolved oxygen near the bottom at 55 m. during spring were lowest off the mouth of the Columbia River (fig. 22). This situation appeared to corroborate the upwelling of deeper water, although biological utilization may have contributed to the low values. Oxygen, like salinity and temperature, followed no significant trend at a particular depth along the Continental Slope.

At 55 m., values of salinity, temperature, and dissolved oxygen in the fall were significantly different from those during spring.

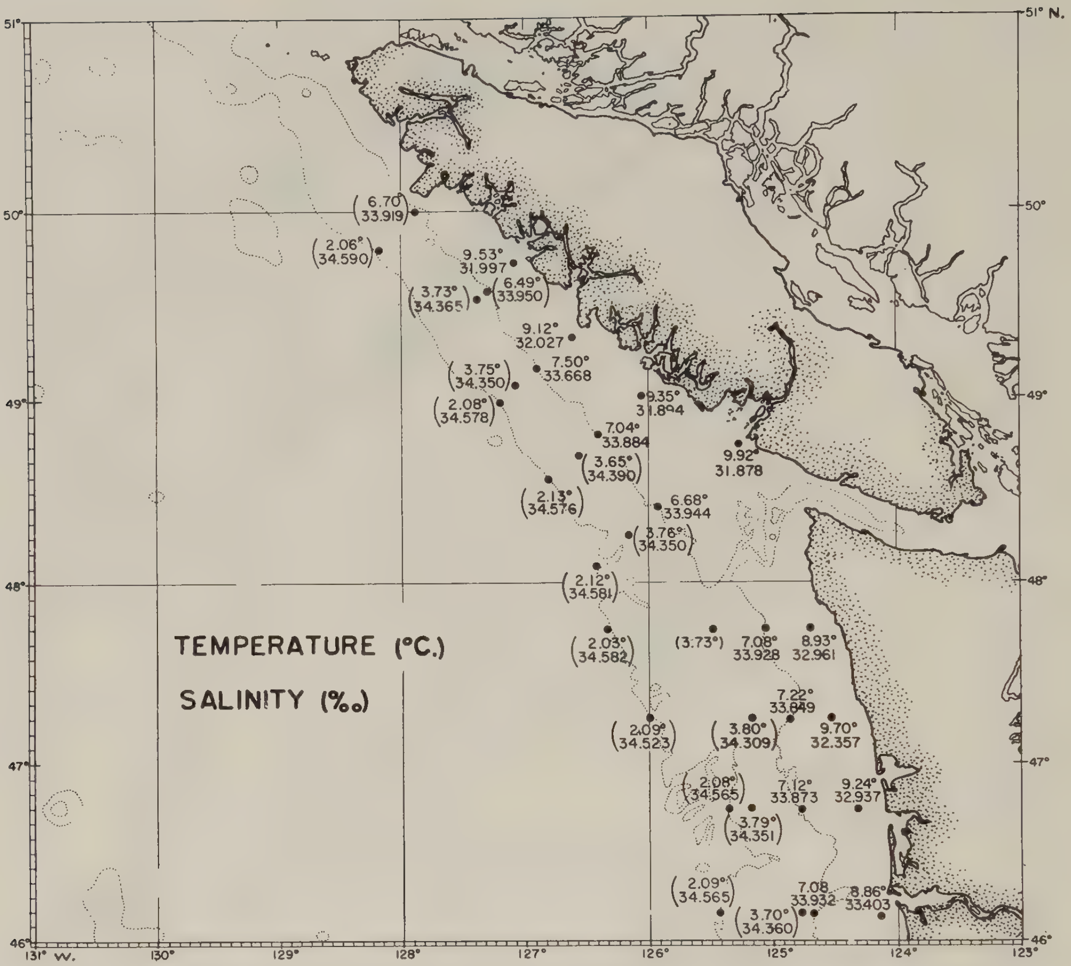
51°
51° N.
50°
49°
48°
47°
46°
131° W.
130°
129°
128°
127°
126°
125°
124°
123°
TEMPERATURE (°C.)
SALINITY (‰)
(6.70° 33.919)
(2.06° 34.590)
9.53° 31.997
(3.73° 34.365)
(6.49° 33.950)
9.12° 32.027
(3.75° 34.350)
7.50° 33.668
(2.08° 34.578)
9.35° 31.894
7.04° 33.884
(3.65° 34.390)
9.92° 31.878
(2.13° 34.576)
6.68° 33.944
(3.76° 34.350)
(2.12° 34.581)
(2.03° 34.582)
(3.73°)
7.08° 33.928
8.93° 32.961
7.22° 33.849
(2.09° 34.523)
(3.80° 34.309)
9.70° 32.357
(2.08° 34.565)
7.12° 33.873
9.24° 32.937
(3.79° 34.351)
(2.09° 34.565)
7.08 33.932
8.86° 33.403
(3.70° 34.360)

FIGURE 21.—Temperature (°C.) and salinity (‰) near the bottom at 55, 183, 914, and 1,829 m. along the continental terrace, spring 1963. (The 183- and 1,829-m. depth contours are shown, and the values in parentheses are interpolated.)

Thus, more uniformity of salinity values — range from 31.6‰ to 32.3‰ — indicated absence of upwelling. By fall, temperatures at 55 m. had increased 3° C. off Vancouver Island, and 4° to 6° C. off the Washington coast. The increase was about 0.6° C. even at 183 m.

DISTRIBUTION OF WATER MASS BELOW 200 METERS

Analysis of distribution of temperature, salinity, and dissolved oxygen indicated significant changes in characteristics of water mass in near-shore areas and also between seasons. Water masses of different character conventionally have been defined by the temperature vs. salinity (T-S) curve plotted from serial oceanographic data (Sverdrup et al., 1942). All T-S curves from spring data were grossly similar; each had a characteristic s-shape and occupied a narrow envelope. The T-S curves of stations farthest offshore were consistently displaced downward toward the left, however. Waters here were colder and less saline than near the coast. The T-S curves from 10 stations within 500 km. of shore along the Willapa Bay-Cobb Seamount line during fall illustrate this displacement (fig. 23). The heavy curves on the lower and right-hand sides are general curves that represent the extreme water masses in the North Pacific Ocean—the Subarctic and Equatorial Pacific Water Masses; they indicate that the coastal water is a mixture of two water masses. The separation

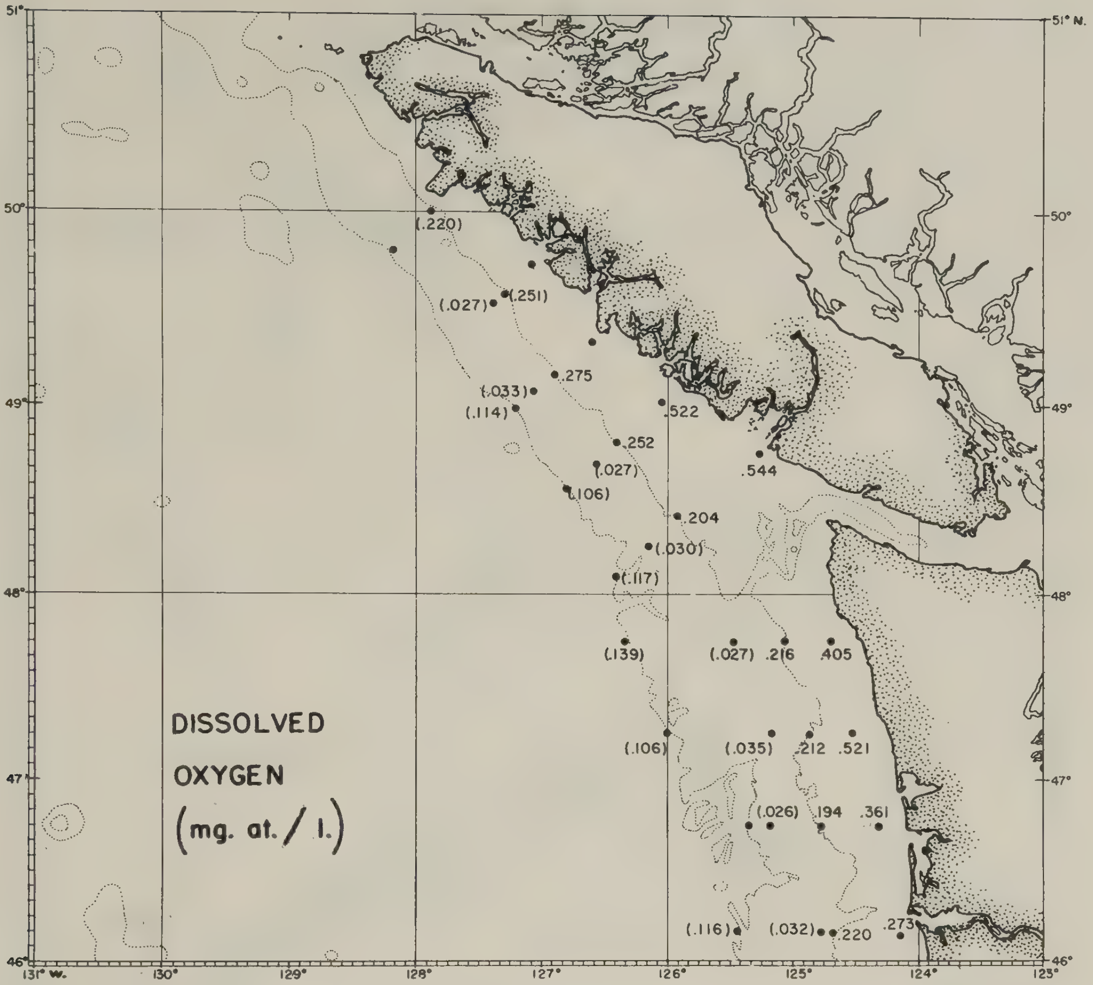

FIGURE 22.—Dissolved oxygen (mg.at./l.) near the bottom at 55, 183, 914, and 1,829 m. along the continental terrace, spring 1963. (The 183- and 1,829-m. depth contours are shown, and values in parentheses are interpolated.)

between the offshore water mass that intrudes from the west and the coastal water mass that intrudes from the south was not distinct at all depths. Near 200 m. three distinct groups of curves existed. Stations 11 to 13 near shore had the most southern characteristics; stations 16 to 19 offshore had the most northern characteristics; and stations 14, 15, and 20 in the center were intermediate between the coastal and offshore water masses. Below 400 m. the boundary between the coastal and offshore water masses was distinct and lay between stations 14 and 15, about 165 to 220 km. from shore.

The study of horizontal changes in the characteristics of water masses throughout the coastal area showed that the differences in temperature were greatest on the salinity surface 34.0‰. Dodimead et al. (1963) suggested that temperatures greater than 6.0° C. on this surface defined the extent of the California Undercurrent Domain which appeared to originate south of lat. 35° N. Their geostrophic calculations, however, indicated only a weak northward flow below 200 m. during 4 of the 5 summers in 1955-59. The temperature distribution on the 34.0‰ salinity surface during spring and fall of 1963 showed the isolines were predominantly parallel to shore although a tongue of warm water apparently entered the area over the Continental Slope from the south. The boundary between the coastal and offshore water masses was marked by a temperature gradient on the seaward side

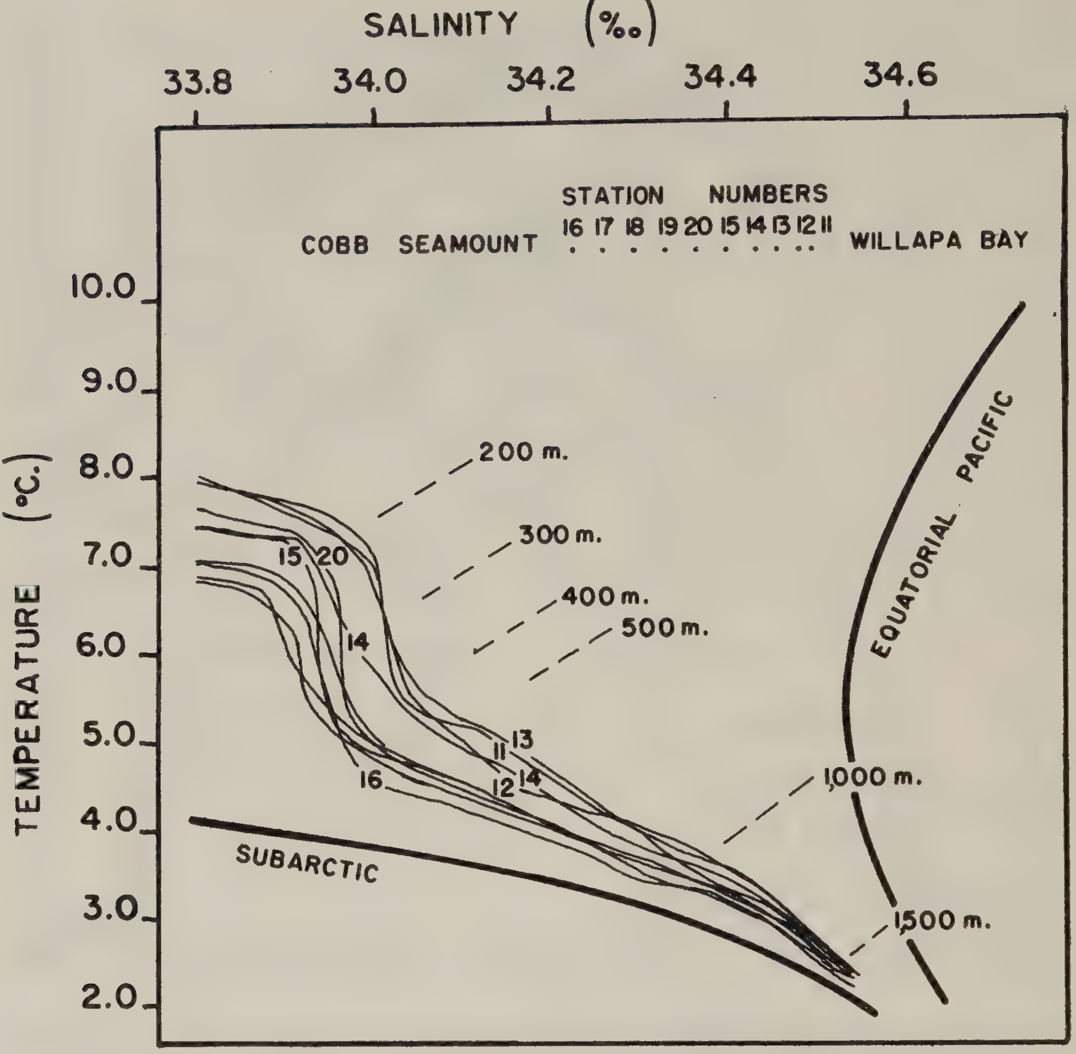

Figure 23.—Temperature vs. salinity curves for water of salinity greater than 33.8‰ between Willapa Bay and Cobb Seamount, fall 1963.

of the tongue. During spring the 6.0° C. isotherm was discontinuous off southern Vancouver Island (fig. 24) where the geostrophic currents indicated onshore movement (fig. 4). The distribution of temperature greater than 6.0° C. showed a band of more southern water about 40 km. wide seaward of the Continental Shelf.

The configuration of the isotherms on 34.0‰ surface was generally similar to the geostrophic currents at 200 m., and the southern water mass was located to the right (if one faces downstream), even when the current was southbound.

The greater area encompassed by the southern water (> 6.0° C.) off the coast of Washington during the fall suggests that the northward flow was greater during fall (fig. 25), but the increased flow was not reflected in the net volume transport.

A more quantitative approach to the description of the distribution of water masses along the Pacific Coast of the United States was made by Tibby (1941) who applied the method of Sverdrup and Fleming (1941) to data obtained by the *E. W. Scripps* in 1939.

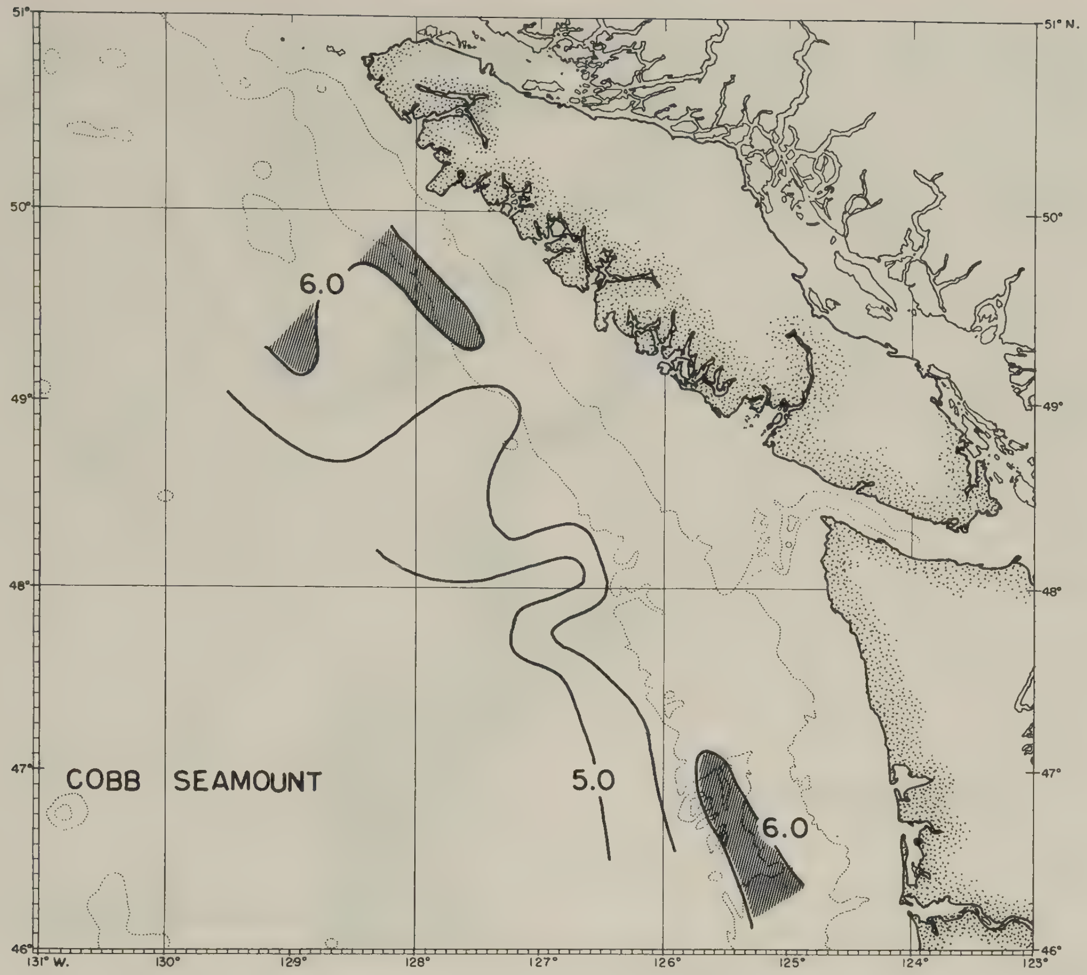

FIGURE 24.—Temperature (°C.) on salinity surface 34.0‰, spring 1963. Shaded portion is above 6.0° C. (The 183- and 1,829-m. depth contours are shown.)

He showed a relatively higher percentage of Equatorial Pacific Water to be present along the Pacific Coast near shore from lat. 25° N. to lat. 45° N. All vertical sections normal to shore showed a greater percentage of southern water toward the bottom and toward shore. The low percentages of southern water in the northernmost sections (between 20 and 40 percent) suggested increased mixing with Subarctic Water to the north.

The percentage of Equatorial Pacific Water off the Washington coast along lat. 46°45′ N. during the fall of 1963 agreed closely with Tibby's results (fig. 26). Because this location is 222 km. farther north than Tibby's most northern line, however, a slightly lower percentage was found. Percentages were not only relatively high near the bottom and near shore, but the high percentages between 200 m. and 400 m. immediately below the halocline extended offshore as far as 500 km. This situation resulted in a pronounced minimum, from 10 to 20 percent, between 600 and 900 m. Values increased sharply within 220 km. of shore. The depth of this minimum percentage of Equatorial Pacific Water coincided surprisingly well with the depth of the oxygen minimum. This determination of distribution of water masses suggests a change in circulation with depth; between 400 m. and 1,000 m., Subarctic Water may move onshore from the west; whereas, between 200 m. and 400 m. and between 1,000 m. and 1,300 m., southern water may move northward along the coast.

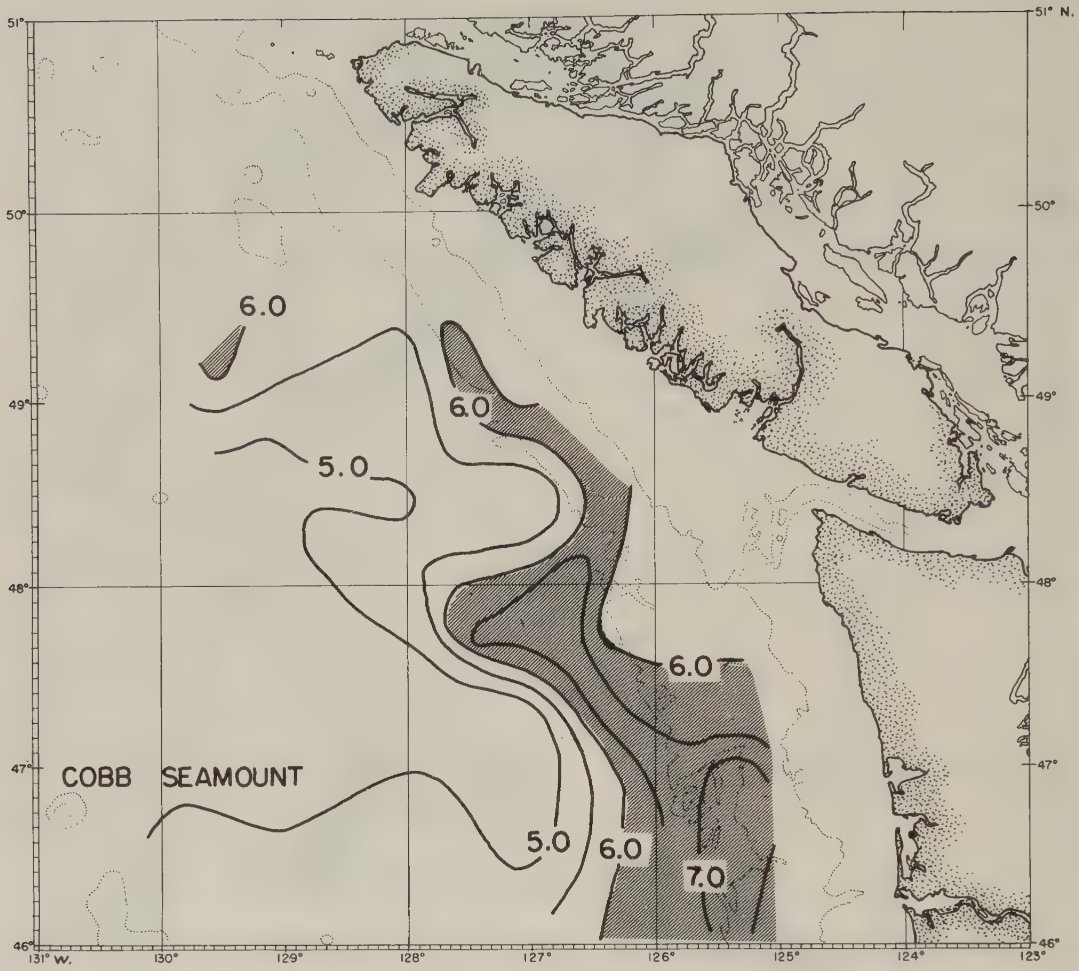

FIGURE 25.—Temperature (°C.) on salinity surface 34.0‰, fall 1963. Shaded portion is above 6.0° C. (The 183- and 1,829-m. depth contours are shown.)

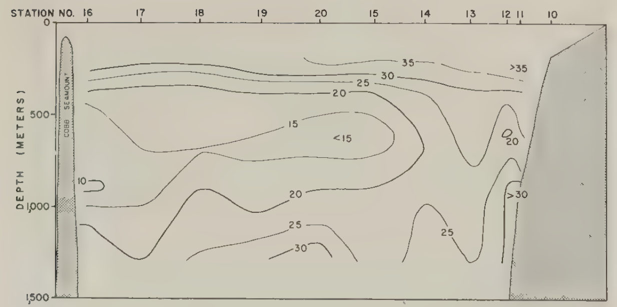

FIGURE 26.—Vertical section of the percentage of Equatorial Pacific Water for water greater than 33.8‰ between Willapa Bay and Cobb Seamount, fall 1963.

SIGNIFICANT OCEANOGRAPHIC FEATURES OF COASTAL WATER

Data obtained during the spring and fall 1963 at closely spaced stations along nine lines normal to shore between the Columbia River and Cape Cook, Vancouver Island, have permitted a description of the significant oceanographic features in the spring within 220 km. of the Vancouver Island and Washington coasts and changes that occurred by the succeeding fall.

Surface geostrophic currents, 0/1,500 db., were similar during both spring and fall. Offshore water flowed northeasterly toward the middle of Vancouver Island and then turned toward the northwest generally parallel to the coast. Eddies off the coast of Washington were such that the northward flow over the Continental Slope, perhaps the Davidson Current, did not appear to continue north of lat. 48° N.

Geostrophic currents, 200/1,500 db., followed the same direction as the surface currents, and showed maxima of subsurface velocity in the eddies off the Washington coast.

The net volume transport, based on a 1,500 db. reference level, was 3 x 10^6m.^{3}/sec. northward past Cape Cook during both spring and fall. A shoreward component of total transport 6.7 x 10^6m.^{3}/sec., was present in the spring, but by fall the transport had reversed to the seaward at 0.4 x 10^6m.^{3}/sec. Northward transport of 4 to 5 x 10^6m.^{3}/sec. occurred locally off the coast of Washington, but was associated with strong anticyclonic eddies which had nearly an equivalent southward transport. Although the existence of the California Undercurrent may be implied by the distribution of properties and supported by the direction of the geostrophic currents at 200 m., the Current did not appear to contribute more than 1 x 10^6m.^{3}/sec. to the net northward flow along the coast of Washington.

The most striking and permanent feature of the distribution of properties within the area was the surface salinity front which extended to a maximum distance of 112 km. seaward from the coast of Washington during the spring, but was confined within 64 km. of the coast in the fall. Vertical sections normal to the shore showed that the major structural features of salinity, temperature, and dissolved oxygen were consistent along each of the nine lines. The distribution of properties varied considerably above 200 m. within the main halocline, thermocline, and oxycline. Below 200 m. the range of values of salinity, temperature, and dissolved oxygen at a given depth was comparatively small. The major feature below the halocline was the nearly horizontal isolines of temperature, salinity, and dissolved oxygen along each vertical section. The concentration of dissolved oxygen had a pronounced minimum at about 900 m. throughout the study area. Minor variations at 200 m. in the fall indicated that a ridge of high-salinity water, also associated with high temperature and low dissolved oxygen, was especially well developed along the Continental Slope of Washington.

Samples obtained near the bottom confirmed the absence of any significant change in the salinity, temperature, or dissolved oxygen at a particular depth along the Continental Slope between the Columbia River and Cape Cook. Thus, the only significant variations in water properties occur in the upper 200 m.

The T-S curves indicated that a water mass of high salinity and high temperature was present over the Continental Slope. Off the coast of Washington the boundary between water masses of slightly different characteristics was distinct below 400 m. between 165 and 220 km. from shore. The more southern water mass near shore occupied a greater portion of the coastal area during the fall than in the spring. Although this implied an increase in northward flow at depth, the California Undercurrent, increased flow was not reflected in the net volume transport.

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SYSTEMATICS AND BIOLOGY OF THE BONEFISH, *ALBULA NEMOPTERA* (FOWLER)[1]

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ABSTRACT

This study is a review of the taxonomic status of the bonefish, *Albula nemoptera,* formerly placed in the genus *Dixonina.* Reasons for synonymizing *Dixonina* with *Albula* are discussed, and it is shown that *pacifica* is conspecific with *nemoptera.* The Atlantic and Pacific populations of *nemoptera* are compared with each other and with the common bonefish, *A. vulpes.* Presumed larval and juvenile stages of *nemoptera* are described and compared with those of *vulpes.* The ecology and distribution of *nemoptera* and *vulpes* is discussed.

Prior to 1911 the family Albulidae was known from several fossil forms and one living species, *Albula vulpes* (Linnaeus). Fowler (1911) described the second living species, *Dixonina nemoptera,* from a single specimen from Hispaniola. Eight years later a second specimen was recorded by Metzelaar (1919) from Venezuela and a third, from the Pacific coast of Mexico, by Myers (1936). A drawing of a specimen from the Pacific coast of Mexico identified as "*Albula vulpes,*" was published by Kumada and Hiyama (1937). According to Walford (1939), apparently several specimens were available to these authors. Beebe (1942), on the basis of 19 specimens from Costa Rica, proposed the name "*Dixonina pacifica*" for the Pacific coast population. The third Atlantic record (Rivas, 1952) was based on two specimens from Jamaica. Recently Caldwell and Caldwell (1964) recorded, tentatively as "*Albula vulpes,*" 14 larvae and juveniles from the Atlantic coast of Panama.

According to the literature, therefore, this apparently rare species of albulid was hitherto known only from four Atlantic records (7 larvae, 6 juveniles, and 4 adults) and the three Pacific records (21 specimens of which 14 are not traceable).

During its cruise No. 92, May 5 through June 17, 1964, the Bureau of Commercial Fisheries exploratory fishing vessel *Oregon* collected 21 adult specimens of *Albula nemoptera* along the Atlantic coast of Colombia. Nineteen of these are available for the present study (see materials and acknowledgments); one was deposited at the Santa Marta Marine Laboratory, Santa Marta, Colombia, and another at the Bureau of Commercial Fisheries Tropical Atlantic Biological Laboratory in Miami, Fla.

Additional specimens from the Atlantic and Pacific, not previously reported in the literature, were located in various institutions.

The fairly adequate material of *A. nemoptera,* now at hand, prompted this study, particularly because the most recent account of the species was based on a single specimen (Hildebrand, 1963) and the conclusions reached therein are open to question (Berry, 1964). In due fairness to the late S. F. Hildebrand, however, it should be remembered that his study was published 14 years after his death in 1949.

We performed this research at the Bureau of Commercial Fisheries Exploratory Fishing and Gear Research Base, Pascagoula, Miss.

MATERIALS

This paper is based on 56 specimens (35 Atlantic; 21 Pacific) of *A. nemoptera* and 43 Atlantic specimens of *A. vulpes* from the

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[3] Present address: BCF Biological Laboratory, Beaufort, N.C.

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collections of the U.S. National Museum (USNM), Stanford University (SU), Field Museum of Natural History, Chicago (FMNH), Los Angeles County Museum (LACM), University of California at Los Angeles (UCLA), University of Miami Institute of Marine Science (UMML), and University of Miami Ichthyological Museum (UMIM). This material is distributed as follows:

A. nemoptera (Atlantic).—Colombia: about 40 km. (22 nautical miles) NW. of Punta San Bernardo, USNM 199530 (3 adults), FMNH 66796 (2 adults); about 22 km. (12 nautical miles) WNW. of Puerto Colombia, USNM 199474 (6 adults), UMIM 5926 (2 adults); about 23 km. (13 nautical miles) NE. of Santa Marta, FMNH 66795 (2 adults), UMIM 5927 (2 adults); about 18 km. (10 nautical miles). WSW. of Puerto Colombia, UMIM 5925 (2 adults). Panama: Caledonia Bay, LACM 20467 (7 larvae, 4 juveniles), LACM 20468 (2 juveniles). Jamaica: Port Antonio, LACM 5802 (1 adult), UMIM 1028 (2 adults).

A. nemoptera (Pacific).—Mexico: Guerrero, Acapulco, USNM 75547 (1 adult); Sinaloa, Mazatlan Playa Camaron, UCLA W51-22 (13 young). Costa Rica: Potrero Grande, SU 46385 (5 young to adult); Gulf of Nicoya, Quepos, UCLA W54-55 (1 adult). Panama: Perlas Islands, Isla del Rey, Punta de Cocos, UCLA W53-285 (1 young).

A. vulpes (Atlantic.). — Florida: Monroe Co., Flamingo, Buttonwood Canal bridge, UMML 16775 (20 young); Dade Co., Miami, UMIM 5917 (2 adults). Bahamas; Cay Sal Bank, Cotton Cay, UNIM 5916 (7 adults). Cuba: Havana, estuary of Guanabo River, UMIM 758 (5 juvenile and young). Jamaica: Port Antonio, UMIM 5918 (1 adult). Colombia: St. Andrews Island, UMIM 5928 (8 larvae).

METHODS

Measurements and counts were made according to methods described by the senior author (Rivas, 1960) with the following modifications and additions. Standard length was measured from the tip of the snout (not the upper lip) to the middle of the caudal base. Prepectoral length was measured from the tip of the snout to the insertion of the appressed left pectoral fin. Head length is the longest distance between the tip of the snout and the margin of the left opercular membrane. Mandible length comprises the distance between the anterior tip of the dentary and the posterior tip of the left articular. Preoral length is the median ventral distance between the tip of the snout and the anterior tip of the dentary with the mouth closed. Body depth was measured at the origin of the dorsal fin. Dorsal and anal fin heights were measured from the origin of the erect fin to the upper tip. Last dorsal and last anal ray lengths were measured between the end of the fin base and the tip of the ray. All the dorsal and anal rays were counted, including the anteriormost short, closely approximated elements. The last two dorsal and anal rays were counted separately. All counts were made from the fish's left side. All pectoral and pelvic rays and all branched caudal rays were counted. All pored scales were counted including those beyond the caudal base. The scales above the lateral line were counted downward and backward from the dorsal fin origin to, but not including, the lateral line. Those below the lateral line were counted upward and forward from the anal fin origin to, but not including, the lateral line. Only the modified predorsal scales, along the midline of the back anterior to the dorsal fin, were counted. The scales around the caudal peduncle were counted at the region of the least depth. All the gill rakers on the first arch were counted, including rudiments; the count for the lower limb includes the gill raker at the angle. All branchiostegal rays were counted. The vertebral counts include the hypural.

GENERIC STATUS OF THE BONEFISH

Largely on subjective grounds the genus *Dixonina* Fowler (1911) is here considered as a synonym of the genus *Albula* Scopoli (1777).

The only two living species of the family Albulidae (*Pterothrissus* not included), *A. vulpes* and *A. nemoptera*, are much more closely related to each other than previously suspected. The differences between them are only of degree and not of the order that would merit generic separation (tables 1–11). Their great superficial similarity is further emphasized by

Table 1.—*Comparison of 21 Atlantic* Albula nemoptera *and 10* A. vulpes *of similar mean length on the basis of differential proportional characters (in thousandths of the standard length)*

[Ontogenetic variation of characters is indicated by symbols in parentheses: (I) isometric, (A+) positively allometric, (A−) negatively allometric]

Character	*A. nemoptera*		*A. vulpes*	
	Range	*Mean*	*Range*	*Mean*
Standard length (mm.)	234–341	289	204–387	293
Prepectoral length (A−)	270–301	286	255–280	268
Preanal length (A+)	824–847	836	835–856	844
Head length (I)	289–312	299	267–296	286
Maxillary length (I)	133–142	138	91–103	94
Mandible length (I)	118–128	123	83– 97	93
Preoral length (I)	43– 49	46	26– 35	29
Orbit diameter (I)	46– 53	50	52– 60	55
Caudal peduncle depth (I)	60– 68	63	70– 78	74
Dorsal base length (I)	173–190	183	138–176	154
Dorsal fin height (A−)	161–177	169	182–197	188
Last dorsal ray length (A+)	152–193	170	54– 56	60
Last anal ray length (A+)	80– 99	89	54– 65	58
Upper caudal lobe length (A−)	204–234	223	232–275	256
Lower caudal lobe length (A−)	187–208	200	216–254	239

Table 2.—*Comparison of 9 Atlantic and 7 Pacific specimens of* Albula nemoptera *of similar mean length on the basis of proportional characters (thousandths of the standard length)*

[Ontogenetic variation of characters is indicated by symbols in parentheses: (I) isometric, (A+) positively allometric, (A−) negatively allometric]

Character	Atlantic		Pacific	
	Range	*Mean*	*Range*	*Mean*
Standard length (mm.)	72–341	246	78–346	205
Predorsal length (A+)	464–490	479	473–513	489
Prepectoral length (A−)	278–301	288	267–294	283
Prepelvic length (A+)	558–602	589	570–610	586
Preanal length (A+)	806–847	829	814–838	830
Head length (I)	297–304	300	280–302	290
Snout length (I)	110–120	115	107–116	111
Maxillary length (I)	133–140	138	124–139	130
Mandible length (I)	119–128	123	111–129	118
Preoral length (I)	43– 49	45	39– 49	42
Orbit diameter (A−)	47– 68	53	46– 67	52
Interorbital width (I)	61– 69	65	61– 66	65
Body depth (A+)	178–199	190	165–208	184
Caudal peduncle depth (I)	60– 70	65	62– 68	66
Dorsal base length (I)	179–194	186	181–204	189
Anal base length (I)	51– 63	58	56– 66	59
Dorsal fin height (A−)	163–192	173	171–194	184
Anal fin height (I)	87– 94	90	88–105	98
Pectoral fin length (I)	142–152	147	141–161	151
Pelvic fin length (I)	114–136	121	120–130	125
Last dorsal ray length (A+)	39–178	150	45–175	130
Last anal ray length (A+)	49– 96	86	54–107	87
Upper caudal lobe length (A−)	204–234	222	217–237	237
Lower caudal lobe length (A−)	187–208	200	212–230	222

Table 3.—*Frequency distribution of dorsal and pelvic rays in* Albula nemoptera *and* A. vulpes

Species	Dorsal rays						Pelvic rays				
	No.	*18*	*19*	*20*	*21*	*Mean*	*8*	*9*	*10*	*11*	*Mean*
A. nemoptera (Atlantic)	28	--	--	3	25	20.9	--	28	--	--	9.0
A. nemoptera (Pacific)	21	--	--	4	17	20.8	1	20	--	--	9.0
A. vulpes (Atlantic)	39	10	29	--	--	18.7	--	3	35	1	9.9

Table 4.—*Frequency distribution of pectoral rays in* Albula nemoptera *and* A. vulpes

Species	Pectoral rays						
	No.	*15*	*16*	*17*	*18*	*19*	*Mean*
A. nemoptera (Atlantic)	28	--	3	22	3	--	17.0
A. nemoptera (Pacific)	21	2	4	10	4	1	16.9
A. vulpes (Atlantic)	35	--	--	2	20	13	18.3

Table 5.—*Frequency distribution of lateral line scales in* Albula nemoptera *and* A. vulpes

Species	Lateral line scales																				
	No.	*68*	*69*	*70*	*71*	*72*	*73*	*74*	*75*	*76*	*77*	*78*	*79*	*80*	*81*	*82*	*83*	*84*	*85*	*86*	*Mean*
A. nemoptera (Atlantic)	22	--	--	--	--	--	--	--	--	--	--	1	1	4	5	5	4	2	--	--	81.5
A. nemoptera (Pacific)	17	--	--		--		--	--	--	--	--	--	2	1	2	5	4	2	--	1	82.1
A. vulpes (Atlantic)	38	1	1	3	6	8	9	3	3	2	2	--	--	--	--	--	--	--	--	--	72.6

Table 6.—*Frequency distribution of scales above and below lateral line, and around caudal peduncle in* Albula nemoptera *and* A. vulpes

Species	Scales above lateral line					Scales below lateral line				Scales around caudal peduncle			
	No.	*8*	*9*	*10*	*Mean*	*6*	*7*	*8*	*Mean*	*16*	*17*	*18*	*Mean*
A. nemoptera (Atlantic)	22	--	18	4	9.2	--	7	15	7.7	19	3	--	16.1
A. nemoptera (Pacific)	19	1	14	4	9.2	--	6	13	7.7	11	7	1	16.5
A. vulpes (Atlantic)	37	5	30	2	8.9	32	5	--	6.1	37	--	--	16.0

Table 7.—*Frequency distribution of predorsal scales in* Albula nemoptera *and* A. vulpes

Species	Predorsal scales												
	No.	*14*	*15*	*16*	*17*	*18*	*19*	*20*	*21*	*22*	*23*	*24*	*Mean*
A. nemoptera (Atlantic)	22	--	--	--	1	3	2	7	8	1	--	--	20.0
A. nemoptera (Pacific)	16	--	--	--	--	4	2	4	5	1	--	--	19.8
A. vulpes (Atlantic)	29	2	--	6	8	4	1	1	2	3	1	1	18.1

Table 8.—*Frequency distribution of lower and upper limb gill rakers in* Albula nemoptera *and* A. vulpes

Species	Lower limb							Upper limb							
	No.	*9*	*10*	*11*	*12*	*13*	*Mean*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*Mean*
A. nemoptera (Atlantic)	28	6	18	4	--	--	9.9	2	11	6	3	5	1	--	7.0
A. nemoptera (Pacific)	21	--	4	9	8	--	11.2	--	--	--	7	8	5	1	9.0
A. vulpes (Atlantic)	39	--	--	8	27	4	11.9	--	--	10	19	5	3	2	8.2

TABLE 9.—*Frequency distribution of total gill rakers in* Albula nemoptera *and* A. vulpes

Species	Total gill rakers										
	No.	*15*	*16*	*17*	*18*	*19*	*20*	*21*	*22*	*23*	*Mean*
A. nemoptera (Atlantic)	28	4	8	7	4	3	2	----	----	----	17.0
A. nemoptera (Pacific)	21	----	----	----	1	5	7	6	1	1	20.2
A. vulpes (Atlantic)	39	----	----	----	3	9	16	8	2	1	20.0

TABLE 10.—*Frequency distribution of branchiostegal rays in* Albula nemoptera *and* A. vulpes

Species	Branchiostegal rays							
	No.	*10*	*11*	*12*	*13*	*14*	*15*	*Mean*
A. nemoptera (Atlantic)	27	-----	-----	-----	14	11	2	13.6
A. nemoptera (Pacific)	21	-----	-----	-----	4	12	5	14.0
A. vulpes (Atlantic)	39	7	11	14	6	1	-----	11.6

TABLE 11.—*Frequency distribution of vertebrae in* Albula nemoptera *and* A. vulpes

Species	Vertebrae													
	No.	*69*	*70*	*71*	*72*	*73*	*74*	*75*	*76*	*77*	*78*	*79*	*80*	*Mean*
A. nemoptera (Atlantic)	20	--	--	--	--	--	--	--	--	3	7	10	--	78.4
A. nemoptera (Pacific)	20	--	--	--	--	--	--	--	--	1	9	9	1	78.5
A. vulpes (Atlantic)	20	10	10	--	--	--	--	--	--	--	--	--	--	69.5

a comparison of their detailed structures. From the characters studied there is more indication of similarity than divergence. The most important differences between the two species are the larger mouth and the longer last dorsal and anal rays in *A. nemoptera*. Other differences were in dentition, certain proportions, meristic characters, and color markings.

Even their ancestry, as reconstructed from fossil material, indicates that *A. vulpes* and *A. nemoptera* should not be considered as representing separate monotypic genera. Frizzell (1965), after studying otoliths, suggested a phylogeny of albulid genera dating back to the Cretaceous. Although he retained *Albula* and *Dixonina* as separate genera, his illustrations, descriptions, and comments indicate that these two genera are more closely related to each other than either is to any of their predecessors. Both *Albula* and *Dixonina* are tentatively shown by Frizzell to be descended from the Eocene-Oligocene genus *Metalbula* Frizzell.

Radiographs of 20 juvenile to adult *A. vulpes* and 40 juvenile to adult *A. nemoptera* indicate that the otolith (sagitta) of *A. vulpes* is more inclined, with respect to the axis of the vertebral column, than that of *A. nemoptera*. This has been confirmed by Don L. Frizzell (personal correspondence).

ALBULA NEMOPTERA (FOWLER)

Dixonina nemoptera Fowler, 1911; 652 (original description); Santo Domingo, West Indies. Myers, 1936: 83–85 (new record; compared with *Albula;* Acapulco, Mexico). Walford, 1939: 119 (identification of drawing from Kumada and Hiyama, 1937; Gulf of California). Beebe, 1942: 45 (compared with *D. pacifica*). Rivas, 1952: 3 (popular account of new record; Port Antonia, Jamaica). Hildebrand, 1963: 143–145 (description; relationship; range; synonymy; Acapulco, Mexico). Caldwell and Caldwell, 1964: 4 (dorsal fin rays; Jamaica). Berry, 1964: 722 (synonymy with *D. pacifica* questioned). Frizzell, 1965: 85 (otolith-based taxonomy, classification, lineage, paleoecology).

Albula nemoptera Metzelaar, 1919: 9 (description; comments; generic separation not justified; Puerto Cabello, Venezuela).

Albula vulpes (not of Linnaeus) Kumada and Hiyama, 1937: (colored plate; Gulf of California). Caldwell and Caldwell, 1964: 4–5 (dorsal fin rays; tentative identification; Caledonia Bay, Panama).

Dixonina pacifica Beebe, 1942: 43 (original description; compared with *D. nemoptera;* Potrero Grande, Culebra Bay, and Piedra Blanca, Costa Rica). Hildebrand, 1963: 144–145 (synonymized with *D. nemoptera;* Acapulco, Mexico). Berry, 1964: 722 (synonymy with *D. nemoptera* questioned).

A comparison of specimens from the Atlantic and the Pacific Oceans (tables 2 to 11) indicates that *pacifica* should not be considered as specifically distinct from *nemoptera*. No significant differences were found in 18 of the 23 proportional characters studied (table 2). In the five characters that show differences (dorsal and anal fin height, last dorsal ray length, upper and lower caudal lobe length) the overlap is quite broad. Tables 3 to 11 show that meristic characters are about the same in the Atlantic and Pacific populations with the exception of the apparent higher number of gill rakers (tables 8 and 9) in the Pacific population. This exception results from the indistinction of the anterior one or two rakers in the larger specimens because of encroachment by the surrounding spinous areas. The Pacific specimens were smaller than those from the Atlantic by an average of 69 mm.; this is about one-fifth of the largest Atlantic (341 mm.) and the largest Pacific (346 mm.) specimens available. In spite of the apparent difference in the number of gill rakers between the Atlantic and Pacific populations, the overlap is broad and the mean difference small. The Atlantic and Pacific populations do not differ in other characters studied, as discussed below. The number of anal rays (9) not shown in the tables is constant in the Atlantic and Pacific populations.

The Atlantic and Pacific populations of *A. nemoptera* appear to differ slightly in the height of the dorsal and anal fins, the length of the last dorsal ray, the length of the caudal lobes, and the number of gill rakers. These differences, however, do not justify separation at the species level and, probably, not even at the subspecies level. The alleged differences described by Beebe (1942) all break down when adequate material is analyzed.

The following is an itemized description of qualitative characters.

Heart.—The heart of one adult Atlantic specimen was dissected. It has two rows of valves in the conus as in *A. vulpes*.

Gular plate.—Hildebrand (1963: 132), the last reviewer, and most preceding authors, stated that a gular plate is absent in the family Albulidae; however, Nybelin (1960: 78) has demonstrated its presence in *A. vulpes*. Following Nybelin's method (alizarine stain), we found that *A. nemoptera* has a gular plate, similar to that of *A. vulpes*.

Dentition.—A detailed description of Pacific specimens' dentition was given by Beebe (1942). Atlantic specimens are in full agreement with that description. As indicated by Beebe, there is considerable ontogenetic variation in the teeth.

Coloration.—The life colors, based on Pacific specimens, were described by Beebe (1942). Two specimens (UMIM 1028) collected in Port Antonio, Jamaica, were in agreement with Beebe's description. Preserved material has longitudinal dark lines, between the rows of scales, especially above the lateral line. There are an elongate black dash anteriorly on each side of the snout and a median anchor-shaped mark on the tip of the snout extending ventrally towards the mouth.

Size.—The largest known specimen from the Atlantic (Colombia, UMIM 5927) is 341 mm. in standard length, and the largest known Pacific specimen (Acapulco, Mexico, USNM 75547) is 346 mm.

Sex ratio.—The 19 Colombian specimens were sexed: 9 mature males and 10 mature females.

Range.—In the Atlantic the species is now known to occur along the Caribbean coasts of Venezuela, Colombia, and Panama, and at Jamaica and Hispaniola. In the Pacific it is known from Mazatlan and Acapulco, Mexico, and from Costa Rica and Panama.

RELATIONSHIPS WITH *ALBULA VULPES*

A. nemoptera and *A. vulpes* differ in several proportional characters, especially those pertaining to mouth structures and to the elongation of the last dorsal and anal rays into a filament in *A. nemoptera* (table 1). These characters, as well as meristic differences (tables 3 to 11) leave no doubt as to the specific distinction between *A. nemoptera* and *A. vulpes*. As already discussed, however, these are differences of degree not to be considered of generic importance. More basic structural characters such as the presence of a gular plate and two rows of valves in the conus arteriosus are common to both species.

Differences in dentition between *A. nemoptera* and *A. vulpes* are, again, of degree. The premaxillary, dentary and palatine teeth are larger in *A. nemoptera*. Also in *A. nemoptera* the premaxillary band of teeth is two or three teeth wide at the symphysis and three or four in *A. vulpes*. The parasphenoid and entopterygoid teeth, however, are larger and fewer in *A. vulpes*. Maxillary teeth are present in juvenile and young adult *A. nemoptera* to about 250 mm. in standard length, whereas maxillary teeth are present only in juvenile *A. vulpes* less than 50 mm.

The only differences in color pattern between *A. vulpes* and *A. nemoptera* are the markings on the snout. In *A. vulpes* there is a median inverted U-shaped mark on the tip of the snout instead of an anchor-shaped mark and there are no lateral black dashes.

Both species are sympatric, but there is evidence that they may be partially segregated ecologically. This is discussed elsewhere in this study.

For purposes of identification and comparison the most significant differences between *A. nemoptera* and *A. vulpes* are summarized in the following key:

1a.—Vertebrae 77 to 80. Dorsal rays 21, rarely 20. Pelvic rays 9. Pectoral rays 16 to 18, usually 17. Branchiostegal rays 13 or 14, rarely 12 or 15. Lateral line scales 78 to 84, usually 80 to 82. Last ray of dorsal fin prolonged into a filament reaching beyond vertical from tip of pelvic fin (except in specimens smaller than 75 mm. in standard length). Last ray of anal fin prolonged into a filament longer than anal fin base (except in specimens smaller than 75 mm. in standard length). Maxillary reaching beyond vertical from anterior margin of orbit.

.... *Albula nemoptera*

1b.—Vertebrae 69 or 70. Dorsal rays 18 or 19, usually 19. Pelvic rays 10, rarely 9 or 11. Pectoral rays 17 to 19, usually 18. Branchiostegal rays 10 to 14, usually 11 or 12. Lateral line scales 68 to 77, usually 71 to 73. Last ray of dorsal fin not prolonged into a filament reaching beyond vertical from tip of pelvic fin. Last ray of anal fin not prolonged into a filament longer than anal fin base. Maxillary not reaching to vertical from anterior margin of orbit (except in specimens smaller than 70 mm., standard length).

.... *Albula vulpes*

EARLY STAGES OF DEVELOPMENT

Seven larval albulids, collected with four juvenile *A. nemoptera* in Caledonia Bay, Panama (LACM 20467) are tentatively identified as metamorphosing larvae of *A. nemoptera.* This identification was determined by comparing these larvae (table 12) with as many of *A. vulpes* of equal size as could be found in Alexander (1961). To avoid misinterpretations resulting from slight differences in measuring and counting, six larval *A. vulpes* of comparable size from St. Andrews island (UMIM 5928) were included as a control.

The presumed *A. nemoptera* larvae differ from those of *A. vulpes* in predorsal length, preanal length, and number of myomeres (table 12). These differences are confirmed by the comparison of juveniles of *A. vulpes* and *A. nemoptera* (table 13). In both species the number of vertebrae is higher than the observed number of myomeres, and this difference is probably due to the difficulty in discerning the last, very closely approximated myomeres especially in *A. nemoptera.* The apparent greater number of vertebrae in juveniles (table 13) is, on the average, three or four units greater than in adults (table 11) as counted from the radiographs, and this difference may

TABLE 12.—*Comparison of metamorphosing larvae of* Albula nemoptera? *and* A. vulpes *of similar size*

[Proportions in thousandths of the standard length]

Character	*A. nemoptera?*		*A. vulpes*			
	Caledonia Bay, Panama, LACM 20467 (7 specimens)		Alexander, 1961: 38–40 (8 specimens)		St. Andrews Island, Colombia, UMIM 5928 (6 specimens)	
	Range	*Mean*	*Range*	*Mean*	*Range*	*Mean*
Standard length (mm.)	58.3- 48.8	51.3	57.0- 48.5	51.4	56.2- 48.0	52.2
Predorsal length	778 –815	795	805 -830	818	807 –825	814
Preanal length	922 –971	944	948 –980	968	956 –975	968
Number of myomeres	69 – 74	70.8	67 – 70	67.8	67 – 69	68.2

TABLE 13.—*Comparison of juveniles of* Albula nemoptera *and* A. vulpes *of similar size*

[Proportions in thousandths of the standard length]

Character	*A. nemoptera*		*A. vulpes*	
	Caledonia Bay, Panama, LACM 20467, 20468 (5 specimens)		Guanabo, Cuba, UMIM 758 (5 specimens)	
	Range	*Mean*	*Range*	*Mean*
Standard length (mm.)	36– 49	43	30– 49	42
Predorsal length	454–467	460	472–490	481
Preanal length	781–793	787	800–817	812
Number of vertebrae	80– 81	80.5	72– 74	73.0

be explained by the fusion of three or four terminal vertebral centra in adults as pointed out by Hollister (1936).

The presumed leptocephali of *A. nemoptera* are identical to those of *A. vulpes* in general appearance. The juveniles, however, are readily distinguished from those of *A. vulpes* by the much larger mouth. The smallest juvenile *A. nemoptera* (Caledonia Bay, Panama, LACM 20468) was 36 mm. standard length. Four other juveniles from the same general locality (LACM 20467) were 42 to 49 mm.

Alexander (1961) stated that variation in total myomere counts (65 to 72) might indicate subspeciation or even separate species; some of her larvae with 69 or more myomeres may be *A. nemoptera.*

ECOLOGICAL IMPLICATIONS

Frizzell (1965) discussed the ecology and distribution of recent and fossil albulids and suggested that competition between *A. vulpes* and *A. nemoptera* drove the latter to deeper water. This conclusion was based on the study of fossils.

In agreement with the above suggestion all adults (about 200 mm. standard length or larger) of *A. nemoptera* for which capture data are available, were collected in relatively deep water. The 21 *Oregon* specimens (234 to 341 mm.) were collected in trawls in depths of 27 to 110 m. The three Jamaican specimens (197 to 265 mm.) were taken with handline in about 37 m. The Pacific specimens reported by Kumada and Hiyama (1937) were taken by a trawl but no exact depth of capture was given. Of the 19 Pacific specimens reported by Beebe (1942: 44), 5 (220 to 365 mm.) were taken with handline from the ship (*Zaca*) at undetermined depths; the other 14 (80 to 200 mm.) were collected with a seine presumably in shallow water close to the beach.

The senior author has been watching for *A. nemoptera* since 1938, and he has examined hundreds of bonefish in museums and especially in the field throughout southern Florida, the Bahamas, and the Caribbean area. All adult *A. vulpes* came from depths less than 2 m. except one (231 mm., UMIM 5918) taken with three *A. nemoptera* from Jamaica. No specimens of *A. vulpes* were taken with the *Oregon* collections of *A. nemoptera.*

The available evidence suggests that there could be a bathic segregation of adult populations of *A. vulpes* and *A. nemoptera* where the latter occupies the deeper stratum. Overlap in their depth ranges is also suggested, but the depth and width of the overlap zone cannot be determined now.

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RESPONSES OF MARINE ORGANISMS DURING THE SOLAR ECLIPSE OF JULY 1963

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ABSTRACT

Biological and physical observations and measurements were made on the day before and on the day of a total eclipse of the sun, July 19–20, 1963. Totality occurred at 1745 hours (e.d.t.), and observations continued through sunset on both days and in two locations—Bar Harbor and Boothbay Harbor, Maine. Plankton was collected at half-hour intervals, and the activity of herring (*Clupea harengus harengus*) and green crabs (*Carcinus maenas*) was recorded every 15 minutes. Collections of physical data included surface and subsurface illuminance, air and water temperature, salinity, barometric pressure, cloud cover, visibility, and tidal data.

At totality and sunset, the volumes of zooplankton in the surface waters decreased. The responses of copepods varied with the species. *Pseudocalanus minutus* and *Acartia longiremis* showed the most pronounced response and moved towards the surface. Females of *Acartia* were more active than the males. The reactions of other zooplankters were either weak or ill-defined. Herring began schooling near the surface at totality; this behavior, though not as strong, was comparable to that observed at sunset. Green crabs were not active during the eclipse, but were very active after sunset. Similarly, strong echo-tracings were documented after sunset but none were recorded at totality. Apparently the duration of the eclipse was too short or the light intensity too high, or both, to elicit responses from some organisms.

Observations from earlier eclipse studies of marine organisms are discussed and comparisons are made with other field and laboratory studies of behavior in relation to environmental changes.

Animal behavior during solar eclipses has attracted the interest of scientists and naturalists, alike, but relatively few observations of aquatic organisms, particularly marine animals, have been published. A discussion of this lack at a meeting of the Oceanographic Committee of the National Academy of Sciences in 1962 provided the impetus to undertake the observations reported in this paper.

The few specific references to aquatic observations during solar eclipses generally failed to include adequate definition of the physical conditions. Wheeler, MacCoy, Griscom, Allen, and Coolidge (1935) reported on the behavior of fishes and amphibians as observed by game wardens and the interested public during the eclipse of 1932 in the United States. These reports included remarks about feeding habits of freshwater "trout" and "minnows," responses to angling lures, and unusual activity such as pickerel jumping out of the water, and a goldfish eating the tail of another in an aquarium. E. E. Dissell (personal communication, Portland, Maine) reported that a school of pollock (*Pollachius virens*) surfaced during the 1932 eclipse—the earliest observation I located for a marine fish. Some of these reports suggest a suppression of activity at totality and others an increased level of activity; but most of the reports were casual observations by laymen and the significance of the observations is limited.

Probably the first carefully planned series of observations was made by Mori (1939), during the 1936 eclipse in Japan. He studied the responses of insects and birds at totality and mentioned the behavior of the sandhopper, *Orchestia* sp., and the migration of eye pigment in the crayfish, *Cambaroides japonicus*. He also included a brief reference to responses of other crustaceans and several fishes. Weber (1952), though mostly concerned with terrestrial organisms, concentrated his efforts on species whose normal behavior was well known and recorded changes in temperature, light, and

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humidity during a 1952 eclipse in Iraq. Petipa (1955) sampled zooplankton during the 1954 eclipse in the Black Sea, U.S.S.R., and reported that most of these organisms responded by rising towards the surface at totality. K. F. Wiborg (personal communication, Bergen, Norway) made studies off the Norwegian coast during the 1954 eclipse, but poor weather—overcast with strong winds—hampered the collection of zooplankton and interpretation of results. Some of the observations made during the July 1963 eclipse have already been reported. Skud (1964) recorded the responses of herring, *Clupea harengus*, and the green crab, *Carcinus maenas;* and Backus, Clark, and Wing (1965) described changes in depth of the scattering layers and the occurrence of bioluminescent flashes.

Though the number of references dealing with responses of marine organisms to solar eclipses is small, there is a considerable background of information concerning reactions to light—both in nature and in the laboratory. The purposes of this article are to present the more detailed observations made during the eclipse of July 1963, to compare these observations with pertinent information from similar studies, and to add to the general knowledge of phototactic responses and rhythmic behavior patterns.

OBSERVATIONS AND COLLECTING METHODS

The total eclipse of the sun occurred on Saturday, July 20, 1963, and the path of totality bisected the State of Maine (fig. 1). At Bar Harbor, mideclipse occurred at 21:45:00 Ephemeris time (17:44:25 eastern daylight time), the sun's altitude was 25 degrees, the path of totality was 53 miles wide, and the duration was 59 seconds (U.S. Naval Observatory, 1961). All of the State experienced at least 98 percent totality. At totality, cloud cover varied considerably along the coast and obstructed viewing in some areas, as did fog patches in certain offshore areas. At Bar Harbor, the 20-m. Fish and Wildlife Service research vessel *Rorqual* was used as an observation and collecting platform; though a light fog reduced visibility on the water surface to a few miles, the eclipse was fully visible. At Boothbay Harbor, the 14-m. FWS vessel *Phalarope* was used to collect samples. Holding tanks were arranged at the Laboratory dock to study responses of organisms held in captivity. Activity of the captive animals was recorded every 15 minutes. All observations are reported as eastern daylight time unless otherwise specified.

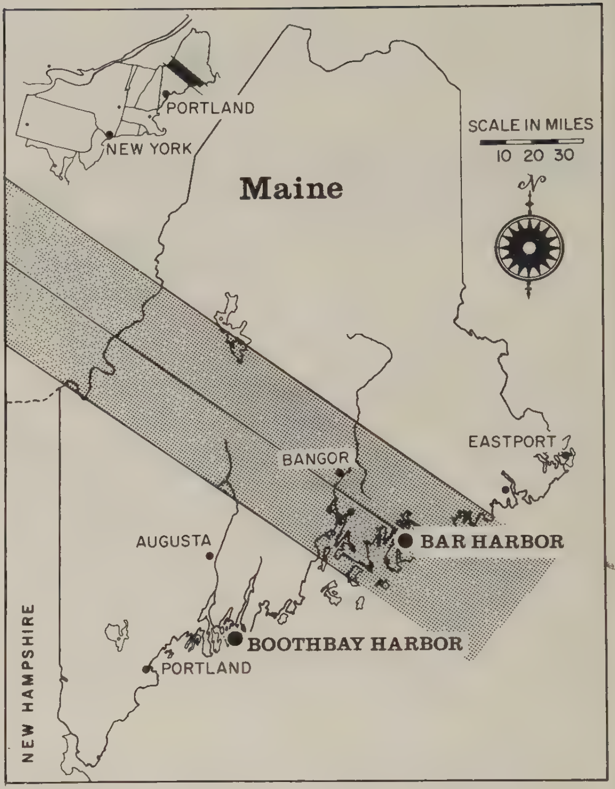

FIGURE 1.—Path of totality and vicinity of sampling areas during solar eclipse of July 20, 1963.

Observations and collections were made on the day previous to the eclipse and on the day of eclipse, beginning at 1600 hours and continuing at intervals through totality (1745) until 2300. The 2-day sequence was intended to provide a test and control in detecting differences in the behavior of animals, as was the extension of observations through sunset and early evening. Light measurements at Boothbay Harbor were made at the surface with a Gossen Lunasix electronic exposure meter.[1] This meter lacked the flat interception screen necessary for precise measurement of illumination, but the incident light readings did provide an index for comparing the illumination between and within days. Aboard the *Rorqual* an irradiance meter (Model C-1a, Marine Advisors, Inc.) equipped with Weston photronic cells measured subsurface changes in light penetration. This unit had a filter with a peak sensitivity of 550 millimicrons and a range of 390 to 760 millimicrons. The irradiance meter provided the ratio of the amount of radiation at the depth of the submerged cell to a reference cell on deck. Secchi-disk readings also were taken at regular intervals. Plankton samples were taken at half-hourly intervals with Miller high-speed samplers at Bar Harbor, and at hourly intervals with the Clarke-Bumpus sampler at Boothbay Harbor. Temperature and salinity were recorded and echo soundings were made continuously during the sampling period.

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[1] Trade names referred to in this publication do not imply endorsement of the products.

PHYSICAL CHANGES

Measurements at Boothbay Harbor showed that illuminances on the day before the eclipse were (control day) and the day of the eclipse was not closely comparable (table 1). Except for the period of totality, surface illumination was far greater on the day of the eclipse than on the control day. This difference was also evident from other data. Visibility on July 19 was limited to 9 km., and nine-tenths of the sky was covered by cirrostratus clouds; on July 20, objects were visible at 16 km. and the stratus cloud cover of seven-tenths was generally dissolving. These differences limited the comparisons which could be made between test and control days.

The decrease in surface illuminance before and at totality and the subsequent increase are documented in table 1. An hour before totality, 75,000 luxes were recorded, 900 at totality, and 28,000 within the hour after totality. Darkness at totality (1745) approximated that which occurred one-half hour before sunset. Though the primary purpose of Secchi-disk observations was to measure water clarity, the results also provided information on the submarine light penetration during the eclipse. The extinction depth of the Secchi-disk was 7.0 m. at 1600,

TABLE 1.—*Surface illuminance at Boothbay Harbor, July 19 and 20, 1963*

Time (e.d.t.)	July 19	July 20
	Luxes	*Luxes*
1546–1600	38,000	>100,000
1601–1615	38,000	>100,000
1616–1630	33,000	>100,000
1631–1645	75,000	75,000
1646–1700	93,000	------
1701–1715	64,000	75,000
1716–1730	------	55,000
1731–1745	24,000	[1] 900
1746–1800	24,000	1,050
1801–1815	11,500	24,000
1816–1830	9,500	28,000
1831–1845	16,750	19,000
1846–1900	4,800	16,600
1901–1915	3,600	16,600
1916–1930	3,600	3,600
1931–1945	900	825
1946–2000	265	[2] 265
2001–2015	110	------
2016–2030	20	50
2031–2045	<10	<10
2046–2100	<10	<10

[1] Totality.
[2] Sunset.

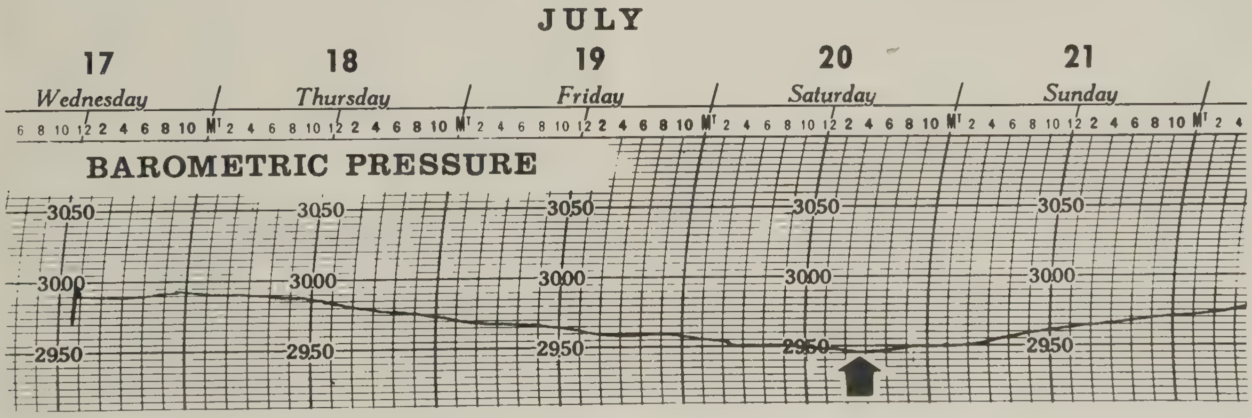

FIGURE 2.—Barometric pressure, mm. of mercury, adjusted to sea level, at Boothbay Harbor. The arrow indicates time of totality.

5.5 m. at totality, 6.0 m. at 1 hour after totality, and 5.5 m. at sunset.

In conjunction with these observations, barometric pressure was measured from Wednesday, July 17 through Sunday, July 21 (fig. 2). Totality coincided with the low pressure reading (29.45 mm.) for the period of observation. The consistent decline in pressure before the eclipse and the rise after totality may or may not be coincidental, but I have been unable to locate similar records from other eclipses.

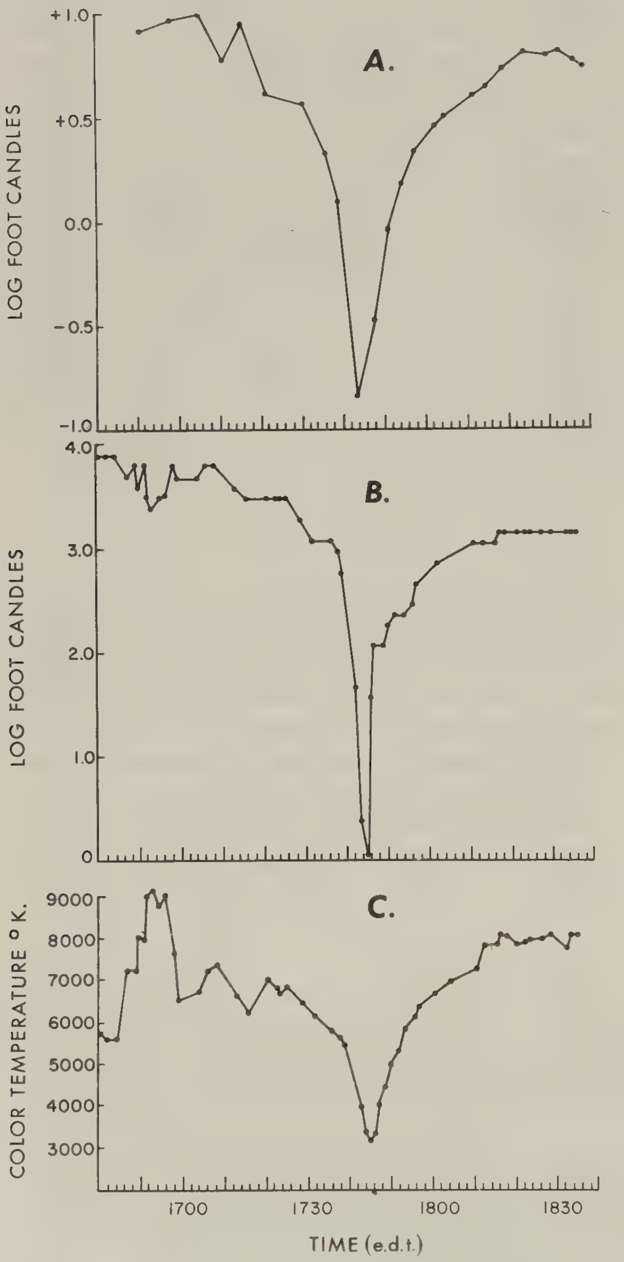

Figure 3.—Time-light curve from: A. photometer; B. Gossen light meter; and C. Gossen Sixticolor meter. (One foot-candle = 10.76 luxes.)

Observations aboard the *Rorqual* in Bar Harbor were supplemented by land-based observations on Mount Cadillac. LFE Electronics (Boston) conducted a series of tests and supplied me with comparative measurements of a time-light series (fig. 3). The differences among the curves are largely due to the different spectral responses of the photo cells and filters. This information provided an independent comparison of our own measurements with the irradiance meter (table 2). Ten minutes before totality, the illumination at the surface registered 4,000 luxes, the lowest value in the series of measurements before and after totality. Subsurface values were also lowest at this time. As is evident from these data, the eclipse occurred during a normal period of declining brightness, but the substantial reduction in illumination at or near totality and the subsequent increase clearly distinguishes the influence of the eclipse. During the eclipse, air temperature declined from 15.3° to 12.5° C., and water temperature at the surface declined from 12.8° to 11.3° C. Though the eclipse may have accentuated the temperature change, the late afternoon decline was anticipated. Water temperature at depth remained nearly constant; 1 hour before totality it was 10.3° C. at 10 meters; 9.3° at 20 m.; 8.3° at 30 m.; and 7.8° at 60 m. Salinity ranged from 31.35 to 31.74 ‰ at the surface and from 32.09 to 32.23 at 60 m. These differences in salinity were assumed to be caused by tidal

Table 2.—*Surface and submarine illuminance (luxes) during the eclipse at Bar Harbor, Maine*

Depth	Time (e.d.t.)				
	1612	1657	1735[1]	1804	1840
Meters	*Luxes*	*Luxes*	*Luxes*	*Luxes*	*Luxes*
Surface	36,000	27,800	4,000	4,800	6,200
5	7,600	5,800	800	1,100	1,500
10	2,600	1,500	400	700	500
15	1,100	700	100	200	150
18	500	300	0	100	100

[1] Totality 1745 e.d.t.

movements. Low tide was at 1646 hours and was -0.08 m.; high tide occurred at 2256, and was 4 m. A light fog sometimes hampered vertical visibility but generally did not obscure the sun.

BEHAVIOR OF ZOOPLANKTON

Cladocerans and copepods were the most numerous zooplankton, accounting for more than 90 percent of the plankters. Less abundant groups included gastropods, brachyurans, and decapod larvae, cirriped nauplii, and chaetognaths. Total volumes of zooplankton and the distribution of seven species of copepods were examined to determine any behavioral changes during the eclipse.

Though the light intensity on July 19 was lower and more variable than on the day of the eclipse, this difference did not totally negate the comparison of zooplankton distribution on the test and control days. Miller high-speed samplers (without meters) were used at Bar Harbor; and Clarke-Bumpus samplers (with meters) at Boothbay Harbor. The zooplankton volumes from surface tows in the two locations are compared in figure 4, along with the changes in light intensity during the 2 days. Although this comparison does not account for amounts of water strained for either gear, the duration of tows in each locale were nearly the same, and the changes in zooplankton abundance which were recorded for the different gears followed similar trends. On both days, the surface volumes of zooplankton decreased at or near sunset and then increased rapidly during the following hour. On the day of the eclipse, a similar decrease was noted at totality, both at Bar Harbor and Boothbay Harbor. This phenomenon was also evident in the quantitative data from the Clarke-Bumpus samplers. Volumes of collections made at the surface were 130 cc./10m.^{3} an hour before the eclipse, 67 cc./10m.^{3} at totality, and 105 cc./10m.^{3} an hour after totality. The decrease in volume also was noted at 20 m.—231 cc./10m.^{3} an hour before totality, 165 cc./10m.^{3} at totality, and 222 cc./10m.^{3} an hour later. At intermediate depths, 3 to 10 m., there was no pronounced change in volume at totality.

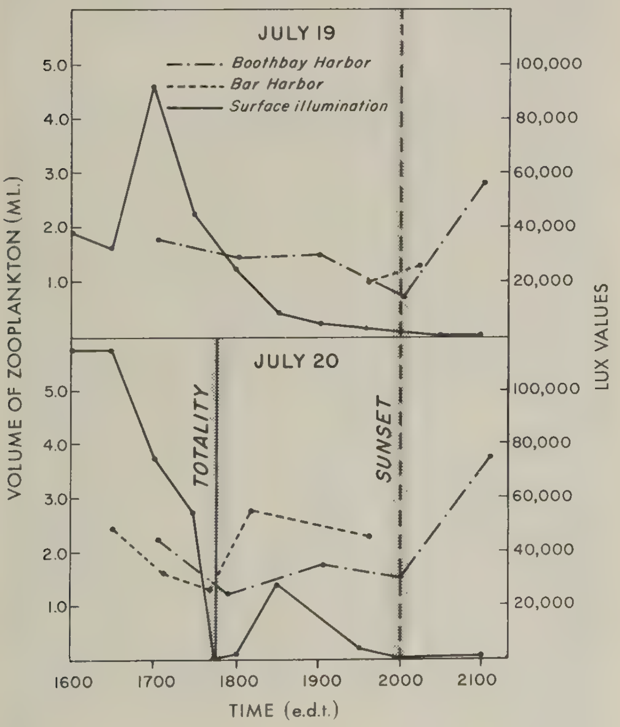

FIGURE 4.—Surface volumes of zooplankton from two sampling locations compared with surface illumination at Boothbay Harbor.

The distribution of seven species of copepods differed measurably on both the test and control days and during the period of the eclipse. On July 19, *Pseudocalanus minutus* and *Acartia longiremis* occupied shallower strata of water than on July 20, which was the brighter day. These species also showed the most pronounced response during the eclipse. The upward movement of these two species and the differences in vertical distribution between days are shown in figure 5. The responses of *Centropages hamatus, Tortanus discaudatus, Calanus finmarchicus, Temora longicornis,* and *Eurytemora herdmani* were not as well defined as those of *P. minutus* and *A. longiremis,* and the responses of some species differed at the two sampling locations. For example, the numbers of *C. finmarchicus* and *T. longicornis* from the surface to 10 m. increased during the eclipse at Boothbay Harbor, but declined at Bar Harbor. The abundance of *E. herdmani* was so limited in Bar Harbor that its distribution could not be plotted reliably; in Boothbay Harbor this species was one of the most abundant

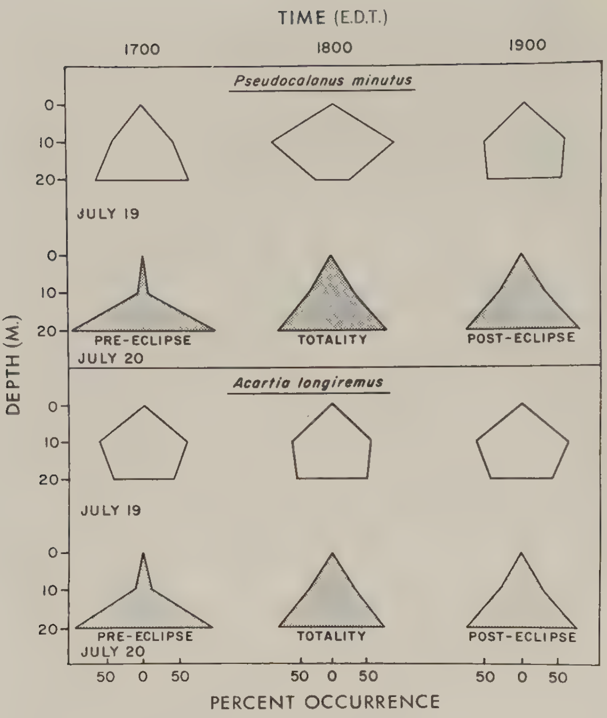

FIGURE 5.—Depth distribution of two species of copepods before, during, and after the eclipse.

forms, but showed no appreciable change in distribution during the eclipse. Though more frequent sampling might have established a basis for understanding these differences, it is evident that all species did not respond in the same degree or in the same manner.

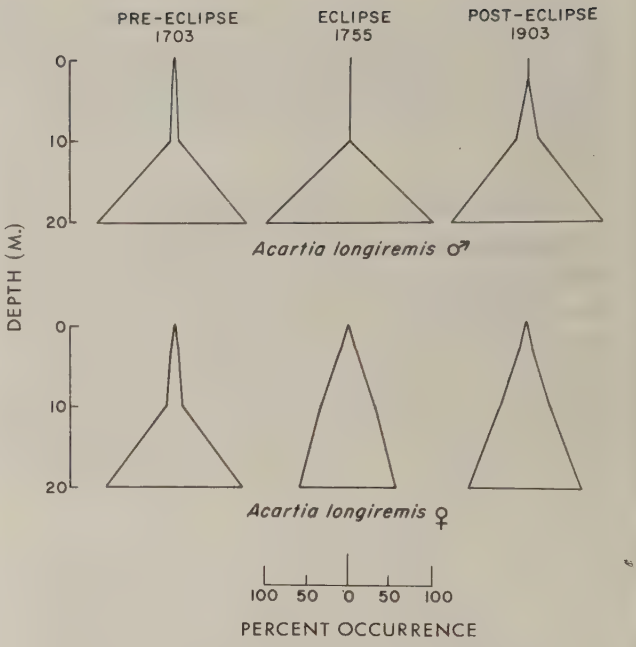

FIGURE 6.—Depth distribution in percent of male and female *Acartia longiremis* during the eclipse.

The lack of uniformity among species and within species was not peculiar to the eclipse study. Wynne-Edwards (1962) summarized several early works which demonstrated the differences in behavior of copepods. Clark (1933 and 1934) discussed diurnal changes in vertical distribution relative to sex and age-groups and reported the stronger migratory habits of adult female *C. finmarchicus*, which rose much nearer to the surface at night than did the male. During the eclipse, female *A. longiremus* were more active than males and were more prevalent at the surface (fig. 6). There was a suggestion of a reversal of this phenomenon in *P. minutus*, and no difference in the distribution of sexes in *T. longicornis*. During the eclipse of 1954, Petipa (1955) reported that vertical migration in the Copepoda was restricted almost entirely to adult females. In all of his samples, females of *A. clausi* were concentrated in the upper layers and the males at lower depths.

BEHAVIOR OF THE GREEN CRAB

Naylor (1958) observed that the rhythmic activity of green crabs (*Carcinus maenas*) could be divided into two components, one of diurnal frequency with a peak at night, and the other, a tidal frequency with a peak at high tide. On the day of the eclipse, low tide occurred an hour before totality and high tide three hours after sunset; consequently the behavior of the crabs could be judged independently of their response to tides.

Thirty crabs, 15 of each sex, were used as test animals. The mean width was 62 mm. (range, 42–79 mm.) for the males, and 60 mm. (range, 51–69 mm.) for the females. The males were banded so that the sexes could be readily distinguished during the experiment. The crabs were placed in a fiberglass tank 1.3 by 1.0 by 0.5 m. that had a 7-cm. layer of sand and gravel on the bottom (fig. 7). One corner of the tank was covered with fiberboard to provide a darkened shelter. Running water

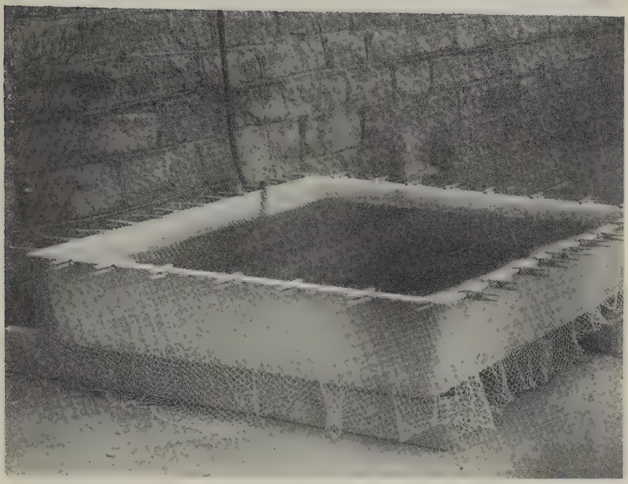

FIGURE 7.—Fiberglass tank for holding green crabs.

was supplied from the laboratory salt-water system and the tank was placed out-of-doors in an area free from shadows. Naylor (1958) found that the normal precision and level of the rhythmic activity declined after the crabs had been held for 3 to 4 days. For my study the crabs were placed in the tank two days before the eclipse and took refuge in the shelter immediately. Activity was recorded by counting the crabs that left this cover. A control was established by making observations periodically during the day before the eclipse and at 15-minute intervals from 1600 to 2200 hours, well past sunset.

On July 19 no crabs left the sheltered area until 2035. From that time until the last observation at 2205 the activity generally increased; as many as 11 males and 10 females left the covered area; the average number of active males was 5.7 and the average number of females 5.2. On the day of the eclipse, July 20, no activity was observed until 2050, more than 3 hours after totality; the greatest number of males in the unsheltered area at any time was 13, and the highest number of females 5; between 2050 and 2200 the average number of active males was 9.2 and females, 3.6.

Because the crabs were not active during the eclipse, other experiments were conducted the following day to determine light conditions which would elicit a response. When the tank was in daylight (27,000 luxes) and then covered by a heavy tarpaulin that reduced the light to less than 10 luxes, 2 minutes elapsed before any activity was noted. Under conditions of subdued artificial light of 500 luxes, which was then reduced to less than 10 luxes, the response was more rapid; 3 crabs were active within 30 seconds and as many as 10 came out of the shelter within 2 minutes. As in the observations made on the date of the eclipse, the males were the first to respond. The light intensity in the half hour before totality was considerably greater than that of the artificial light; apparently the duration of subdued light during the eclipse was too short or the intensity too high to elicit a response from the crabs.

BEHAVIOR OF HERRING

Generally, the behavior of Atlantic herring *(Clupea harengus harengus)* is well documented, but specific responses are extremely variable. Blaxter and Parrish (1965), studying vertical movement, concluded that it was not possible to show any relationship between the preferred depth, or the extent of upward movement, and such factors as gradients of salinity, temperature, or food. The herring used in the eclipse study had been held in large tanks for several weeks. Though their behavior could not be considered comparable to that of herring in their natural environment, the fish were acclimated to confined conditions which were necessary for the observations made during the eclipse.

About 75 two-year-old herring were placed in a small-meshed holding pen during early morning of July 19. Observations were made at 15-minute intervals from 1600 to 2200 hours on July 19 and 20. The pen (dimensions, 3 by 3 by 2 m.) was visually separated into quadrants A, B, C, and D (fig. 8). Each quadrant was divided into two sections by an imaginary plane midway between the surface and the bottom of the pen. The presence or absence of fish in these quadrants and the depth divisions were recorded, along with remarks on schooling and directional movement. On both days, there

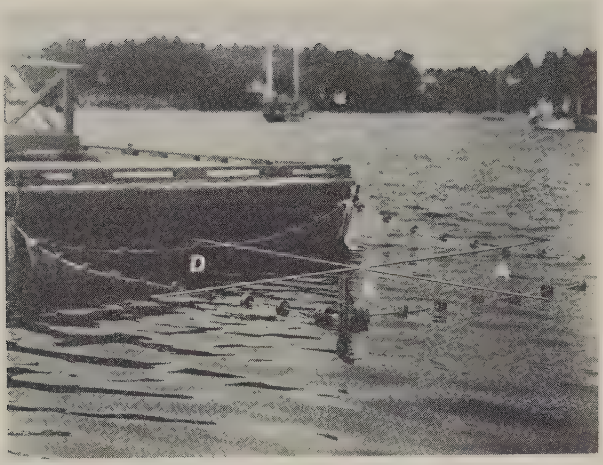

FIGURE 8.—Impoundment for herring, showing quadrants used to record observations.

was only one period (30 to 45 minutes) during which no fish were in the upper layer; this distribution occurred about an hour before sunset (2000). Similarly, there was only one period during which no fish were located in the lower layer. This period began one-half hour after sunset and continued for 45 to 60 minutes, after which herring were dispersed throughout the holding pen.

During daylight herring were more numerous in the upper area of quadrants A and B than in C and D. This difference probably is explained by the uneven distribution of light. Quadrants C and D were located closest to the vessel float which was used to anchor the holding net. The upper areas of these quadrants were shaded by the float and were avoided by the fish. The distribution of herring in the lower layers of A-B and C-D was relatively uniform. After dark, fish were equally dispersed in the upper and lower layers of the pen.

On the day of the eclipse, fish were distributed in the upper layers of quadrants A and B and in the lower layers of quadrants A, B, C, and D. Fish were absent from the upper layer of quadrant D until sunset. No fish were observed in the upper layer of quadrant C from the start of observations at 1600 until 1730—15 minutes before totality. Fish were active in this quadrant from 1730 until 1800; were absent at 1815; and reappeared from 1830 to 1900. This movement of fish into quadrant C at the approach of totality was coupled with a change in behavior of herring in the other quadrants. Some fish began to school and moved to the surface of the water. This was in contrast to the preeclipse behavior of general dispersion without movement at the surface, and apparently was in response to the reduced light during the eclipse. The response was not strong, and not all fish reacted to the change. The data on subsurface illumination (mentioned above) suggests that the duration of lowered light intensity at totality was not enough to stimulate a stronger response. This conclusion is supported by the observations at sunset, when the decrease in light approximated that of the eclipse, but for a longer period, and elicited a stronger schooling response from the herring.

ECHO SOUNDINGS

Echo sounders aboard the two vessels were run continuously during the study, but none of the records showed any change or movement of organisms during the eclipse. Echo tracings in Boothbay Harbor documented considerable activity in the early evening on July 19 and 20 (fig. 9). On July 19, activity was first detected at 1854 when minor peaks and streaks extended up from the bottom. By 1955, some of these streaks and dots were no longer in contact with the bottom; others remained in contact but were extended and more pronounced. By 2100, only a few of these marks were in contact with the bottom; the rest were scattered from the bottom to the surface. This phenomenon was also recorded on the evening of July 20, though somewhat later and less pronounced than on the previous evening.

None of the organisms taken in the plankton nets was large enough to account for the markings observed on the recording paper, and the scheduled collections did not allow time to utilize other gear on July 19 or 20. On July 21, a trawl was fished during late evening in the same area. Echo soundings were similar to those on July 19 and 20. Large catches of jellyfish *(Aurelia aurita)* were taken in the net; presumably they were the animals detected by the sounder, but the possibility exists that the tracings were from herring or other fish that escaped capture. In any case, the lack of response from these organisms during the eclipse indicated that the lowered light intensity or duration of totality, or both, were not sufficient to stimulate the kind of movement observed after dark.

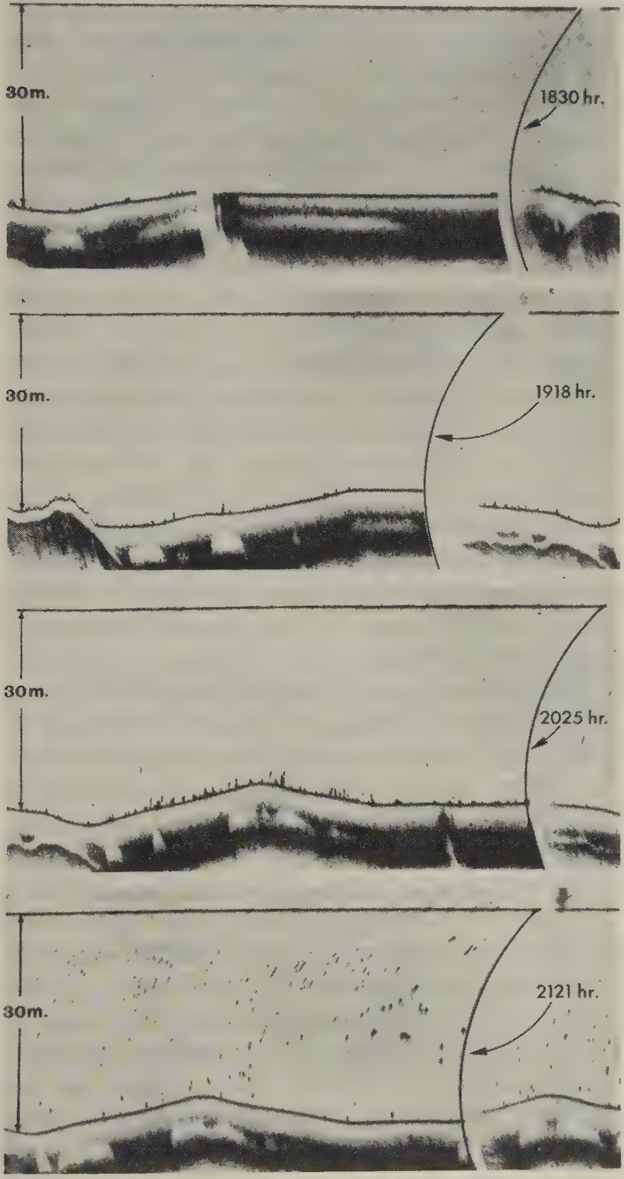

FIGURE 9.—Echo soundings before and after sunset (2000 hr.).

COMPARISON WITH OBSERVATIONS FROM OTHER ECLIPSES

The observations presented in this paper show some agreement with those of previous workers, but the responses recorded for some species were not the same. Considering the variables such as light intensity, duration of totality, and the variation in experimental design, these differences are not surprising, but they should be equated.

Mori (1939) conducted carefully designed experiments on several species, and made detailed observation on others, including the sandhopper, *Orchestia* sp. He concluded that sandhoppers "were apparently not affected by the eclipse," yet he does mention that a few individuals were exposed "towards the end of totality . . . . ," exhibiting their normal crepuscular behavior, but this activity lasted only a few seconds before the animals retreated into hiding. Totality during the 1936 eclipse in Japan lasted 2 minutes, and began at 1519 when illuminance under normal conditions is high. As Mori stated, the inactivity may be explained by the fact that the change of light intensity at totality was too rapid; but he also cautioned that factors such as humidity and atmospheric pressure might have been the controlling influences. He also reported on observations from the aquarium of the Akkesi Marine Biological Laboratory, ". . . shrimp, a flat fish, a young salmon, a trout, and a herring were all indifferent to the eclipse, whereas a crab, which is quiet on ordinary days, began to move, and a bullhead appeared from the shady tangle of weeds when it became darker and hid again when it became lighter in just the same way as seen on ordinary days and nights."

In reference to light-dark cycles, Bünning (1964) stated that deviations from the natural frequency of an organism could "necessarily have an entirely different relationship to the light and dark period than normally. For example, if the dark period is too short, the organism with its own cycle length does not have time enough within the dark period to reach the usual physiological state typical of night." He also stressed that sometimes the beginning of the light period has a greater influence on the timing of responses during dark than the beginning of the dark period itself.

Other factors could also contribute to the degree of response. Of particular interest is the barometric pressure. As shown in figure 2, the pressure declined continuously for the 2 days preceding the 1963 eclipse. Brown (1958) showed that cycles of activity in certain organisms fluctuate with changes in pressure. These species included the fiddler crab (*Uca*), the oyster (*Ostrea*), and the quahog (*Venus*). Though these animals also exhibit daily and lunar cycles of activity, mean hourly rates of activity were correlated with the rates of rise or fall in barometric pressure. Activity increased with the hourly rate of fall and decreased with the rate of rise. The importance of this phenomenon to the observations during the 1963 eclipse is uncertain; it could be of significance during an eclipse with a relatively long period of totality.

In comparing the responses of zooplankton during the eclipses of 1954 and 1963, the importance of documenting the environmental differences is readily apparent. Petipa (1955) reported that most species reacted by rising to the upper water layer (0-5 m.) during the eclipse and by descending to lower depths (5-14 m.) after the eclipse. The strongest response was from *Sagitta,* and larvae of Decapoda, Lamellibranchia, and Gastropoda. His work was done in the Black Sea at Sevastopol Bay where surface temperatures during the eclipse (June) were at least 20° C. Zenkevitch (1963) described the general hydrological features of the Black Sea: salinity varied between 17 and 18 ‰ at the surface and was only 22 to 23 ‰ in deep water; temperature at 25 m. was 14° C. in summer and 6° C. in winter; dissolved oxygen content ranged from 1.05 to 7.76 $cm.^3/l.$ at 50 m. and declined rapidly with increasing depth below 50 m.; water deeper than 150 m. was contaminated with hydrogen sulphide; Secchi disks disappeared between 18 and 21 m.; and most species of zooplankton were found at depths above 50 m. and were concentrated between the surface and 25 m. Many of these characteristics are strikingly different from those in the coastal waters of the Gulf of Maine: during the eclipse of July 20 the temperature was less than 15° C. at the surface and was 10° C. at 10 m.; salinity was about 32 ‰; and the Secchi disk disappeared at less than 10 m. The dissolved oxygen content in the Gulf of Maine was reported by Gran and Braarud (1935) to vary between 5.5 and 7.8 $cm.^3/l.$ at 40 m., and Bigelow (1926), in contrast to the conditions in the Black Sea, reported many species of zooplankton below 50 m., some of which had their densest concentrations below 100 m.

Other differences to consider include the characteristics of the eclipse and the location of sampling in relation to the path of totality. The sampling sites in Maine were selected because they lay in or near the path of totality. In contrast, Sevastopol Bay was about 400 miles from the path of totality in 1954. (This figure was estimated from eclipse data presented by Oppolzer, 1962.) As Petipa (1955) did not provide any measure of light intensity, one can only assume, other things being equal, that the illuminance during the eclipse was higher at Sevastopol than at Bar Harbor. Yet Petipa recorded more activity of zooplankton than was noted in the Gulf of Maine. Differences in species were important, but I suspect that the differences in the two environments were more critical.

Though not a species encountered in this study, experimentation on *Daphnia* offers several plausible explanations for the zooplankton behavior observed during the eclipse. Harris and Wolfe (1955) found that *Daphnia* responded rapidly to changes in light intensity, moving in the direction of the original optimum intensity, but this was followed by movement towards an adapted optimum and resulted in little change of position. In essence, a high change of intensity produced an alteration of photonegative and photopositive phases, and the net result had relatively little effect on the depth at which the animal was located. When changes in light intensity were slow, however, the animals simply followed the movement of the original optimum zone. Ringelberg (1964) disagreed with the explanation of the phototactic response offered by earlier workers; he concluded, on the basis of a very thorough laboratory and field study, "that the directing stimulus for the phototactic reaction is a contrast or a gradient present in the angular light distribution." Schallek (1943) reported that *Acartia tonsa* in a glass cylinder would move upwards when illuminated from above and downward when illuminated obliquely. He considered the reaction of *A. tonsa* to diffuse light in the cylinder to be in accord with the downward movement in the ocean during the day, but that the reaction to direct light under experimental conditions had no bearing on its behavior in nature.

These experiments emphasize the importance of other variables that one must consider in attempting to compare and evaluate observations during an eclipse. The time of day and resultant attitude of the sun in relation to water clarity are of particular concern. Holmes (1957) discussed the penetration of water by light and explained that "The extinction of daylight in the sea is caused by absorption (by the water itself, by particles, and by dissolved substances) and by scattering (by the water and by particles)." Ringelberg (1964) and Schwassman and Hasler (1964) have recognized the importance of absorption and scattering on the phototactic behavior of aquatic organisms; the former paper referred to *Daphnia*, especially the orientation of the eye axis and the body axis, and the latter referred to sun orientation of fishes.

The responses of herring observed during the 1963 eclipse were in general agreement with reports of other observations under varying conditions of light intensity. Johnson (1939) studied captive herring in southern New Brunswick and concluded that, in the absence of direct sunlight, these fish "extended to the surface at all times—dawn, sunrise, cloudy days, sunset, dusk, moonlight, starlight, and cloudy nights." He also found that during daylight, the depth of the fish was greatest when the sun's altitude was highest and the largest fish were in the deepest water. Blaxter and Holliday (1963) summarized the work of European scientists, particularly in the North Sea where the diurnal migration pattern of herring is well documented; and the depth of herring shoals has been correlated with isolux lines to estimate the optimum depth for setting gill nets.

In studying diurnal changes in behavior of adult herring, Blaxter and Parrish (1965) found that the depth (and light intensity) at which the fish occurred during the day was extremely variable; and demonstrated that fish did not move towards the surface until illuminance decreased to 10 luxes. These authors also reported that "recruit fish (2½–3 years old)" remained in higher light intensities by day. The eclipse study lends support to this latter conclusion. Though the response of 2-year-old herring at totality and at sunset was limited, the light intensity was above the level that Blaxter and Parrish observed as necessary to elicit a surface movement by adults. Breder (1951 and 1959) discussed the influence of light on the social grouping of many species of fish and provided a thorough summary of other scientists' work in this field. He stressed the differences in responses by individuals, by sex, and by species. This emphasizes the need to select species whose behavior patterns are well known, when attempting to evaluate the effects of a solar eclipse. The Atlantic herring, in this regard, is a suitable species, except that the sexes cannot be distinguished readily through external examination.

Mention should be made of the types of periodic activity and their importance to the observations made during the eclipse. Allee, Emerson, Park, Park, and Schmidt (1949) classified successive diel periods into two types: exogenous, "in which the pattern is directly induced and controlled by periodic environmental influences" and endogenous, "in which the pattern is resident in the organism." Aschoff (1960) elaborated on the definitions, explaining that an environmentally controlled periodicity (exogenous) will cease under artificially constant conditions; whereas, periodic factors of the environment only serve as synchronizing agents (Zeitgeber) for circadian or endogenous periodicity. He pointed out that a single environmental event can never synchronize continuously and therefore cannot operate as a Zeitgeber. This implies that observations made during an eclipse should not, of themselves, be used to determine whether a response or lack thereof is indicative of either an exogenous or endogenous rhythm. On the other hand, these observations can provide supporting evidence for laboratory or other field experiments concerned with rhythmic behavior patterns. Cloudsley-Thompson (1961) cautioned that rhythmical activities of an animal are not necessarily all of one type and stated that rhythms solely dependent on the environment are rare and probably represent rhythms which are independent but out of phase with the environment. In regard to field observations during solar eclipses, he concluded that the results agree with those of laboratory experiments, in that certain animals exhibit some periodic activities that appear to be dependent on the environment and others that are more markedly independent.

SUMMARY

1. A total eclipse of the sun occurred in Maine on July 20, 1963. Totality lasted 59 seconds.

2. Biological and physical observations were made on the day before the eclipse and the day of the eclipse and were continued through sunset each day to provide a comparison with regular light-dark cycles.

3. Surface and subsurface illuminance declined markedly at totality, approximating conditions at sunset.

4. Barometric pressure declined steadily for the 2 days prior to the eclipse, reached a low point 29.45 mm. at totality, and then increased.

5. Zooplankton volumes from surface waters decreased during the eclipse and at sunset at both of the sampling areas.

6. Of the dominant copepods, *Pseudocalanus minutus* and *Acartia longiremis* exhibited the most pronounced response to the eclipse and moved toward the surface. The reactions of other species were either weak or ill-defined.

7. Female *Acartia longiremis* were more active than males during the eclipse, and moved toward the surface at totality.

8. No change was observed in the behavior of green crabs during the eclipse. Apparently, the duration of the eclipse was too short or the light intensity too high, or both, to elicit a response.

9. At totality, Atlantic herring held in a pen responded in a manner comparable to that observed at sunset. The response was not strong, but some fish began schooling and moved into the surface waters.

10. Echo tracings documented a movement toward the surface after sunset, but tracings during the eclipse showed none of this activity. Though large catches of jellyfish were taken, the traces could have been made by fishes which escaped the net.

11. Comparisons of my observations with those made during other eclipses emphasize the importance of designing experiments carefully to assess properly the behavioral responses in relation to environmental changes.

ACKNOWLEDGMENTS

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SHELL DEFORMITY OF MOLLUSKS ATTRIBUTABLE TO THE HYDROID, *HYDRACTINIA ECHINATA*

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ABSTRACT

The colonial hydroid, a common epizoon on the external surface of the shell of the sea scallop, *Placopecten magellanicus*, sometimes becomes established on the internal shell surface. This intrusion interferes with the normal activities of the scallop's mantle, often causing shell deformity. The scallop reacts by producing a new shell edge within the existing perimeter of the shell and bypassing the hydroid colony. This relation is amensal—one organism is inhibited, and the other is not affected. No proof was found that the hydroid may ultimately cause the death of the scallop.

These same hydroids, in symbiotic association with pagurid crabs, deform and enlarge the apertures of empty gastropod shells. Enlargement of the "house" is to their mutual advantage.

The availability of surface on which to attach and grow is vital for sessile fouling organisms. The larval forms of these species must eventually settle on firm substrate or perish. The organisms are often able to augment available substrate by settling on the surface of other organisms. The upper valve of the sea scallop, *Placopecten magellanicus* (Gmelin), provides such a surface.

Organisms found on shells of sea scallops are those which are found on any suitable substrate in the vicinity. They are commensals, typical epizoa competing for space. They may be pelagic and settle by chance in a particular area, or benthic and possess mobility during larval and early postlarval stages.

Postlarval commensal species found on the sea scallop include representatives of most marine phyla (Merrill, 1961). Most abundant are the boring sponges, sea anemones, branching and encrusting hydroids and bryozoans, pelecypods, barnacles, tubeworms, and simple and colonial ascidians. Wells and Wells (1964), reporting on a calico scallop, *Aequipecten gibbus* (Linnaeus), community study, made similar observations. They found that of the major taxonomic groups only Asteroidea and Ophinoidea were lacking on calico shells.

Most of these animals have a casual association with the sea scallop. They may gain to some extent in having a shell substrate on which to live and possibly by having particles of food brought to them by water currents produced by the scallop. Although the commensal may cause little inconvenience to the host, the scallop certainly does not appear to benefit from the association. In fact, the association may be detrimental to the scallop if extensive fouling of the shell hinders swimming, or if marine borers excavate excessive quantities of the shell; but usually the association provides neither advantage nor harm to the participants.

An association in which the sea scallop is placed at a distinct disadvantage was observed during routine sea scallop studies. The colonial hydroid, *Hydractinia echinata* (Fleming), which grows frequently on the external shell surface of the sea scallop, was observed occasionally to expand around the shell periphery and invade the internal shell surface. The forward elements of the colony, coming in contact with the mantle of the scallop, caused certain inhibitory reactions by the scallop. This paper describes the association, emphasizing the means by which the scallop reacts to internal

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shell invasion. This type of relation in which one of the associates is inhibited while the other is not affected is best described by the term amensal as defined by Odum (1953).

BRIEF REVIEW OF THE LIFE HISTORY OF *HYDRACTINIA ECHINATA*

Hydractinia echinata is far less exclusive in its choice of habitat than earlier observers indicated. It has been dredged "on every sort of bottom" (Sumner, Osburn, and Cole, 1913), and has been found on a wide variety of substrate (Hargitt, 1908). Bunting (1894) mentioned that the hydroid lives on the sea mussel, *Mytilus edulis* (Linnaeus), and Moore (1937) recorded its occurrence on the shell of another bivalve, *Pectunculus* (=*Glycymeris*), but I have seen no other reports of the association of this hydroid with a specific bivalve.

Hydractinia echinata is the well-known hydroid which served formerly as the classic example of symbiosis with the hermit crab, *Pagurus bernhardus* (Linnaeus). Many papers have dwelt on the symbiosis of pagurids and actinians (see Balss, 1924, and Dales, 1957 for a summary of the literature). From experimental studies, however, Schijfsma (1935) concluded that the association of *H. echinata* and *P. bernhardus* could not be defined as true symbiosis—that the hydroid is merely an epizoon.

Schijfsma (1939) described the early stages of growth of colonies of the hydroids, and Fraser (1944) and others have reported in detail the specialization of individuals that make up a colony of *Hydractinia echinata.* This hydroid is polymorphic. Several types of zooids develop, including special generative zooids that produce male and female sporosacs. The ova are fertilized in situ, and after being discharged sink to the bottom where they develop into mobile planulae in 24 to 48 hours. The planulae are never free-swimming; rather they crawl or glide in the manner of turbellarians. The mobile phase lasts at least 24 hours, ending when the planulae fix themselves to a substrate and develop into typical tentacular zooids.

The surface of a sea scallop shell can act as a base for settling planulae. Once attached, the zooids grow from a stoloniferous network of anastomosing tubes to develop into a colony. The coenosarcal expansion is covered with a heavy, chitinous perisarc from which rise the ridged and jagged spines characteristic of the encrusting colony. Nutritive zooids are the most numerous; other types include defensive, sensory, and generative zooids. The mature colony appears as a reddish velvety covering, but feels rough to the touch because of the numerous spines. Batteries of nematocysts in the zooids protect the colony.

ASSOCIATION OF *HYDRACTINIA ECHINATA* AND *PLACOPECTEN MAGELLANICUS*

The size of a colony of *Hydractinia echinata* on the sea scallop varies with the length of time the colony has been established and with the surface area available. Where there is ample surface for expansion, the zooids in the advancing front of the colony tend to be arranged in concentric rows corresponding to the growth marks on the shell. This arrangement was observed by Frederick M. Bayer (personal communication) of the University of Miami, Fla., to whom material was sent for identification; his finding agrees with remarks by Schijfsma (1939) that the course of stolons is influenced by the surface sculpture of the substrate. The colony, by advancing more rapidly than the scallop grows, may eventually arrive at the periphery of the shell and continue around the shell edge. Long, slender zooids, armed heavily with nematocysts, are especially abundant at the advancing edge. Ultimately, the forward elements of the colony come in contact with the extended mantle of the scallop. The mantle withdraws, presumably because of the nematocysts discharged into it.[1] The mantle retreats steadily as the hydroid colony encroaches inward (fig. 1, a–d). Evidence of this sequence is seen clearly in figure 1, a. To be noted are the numerous relatively

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[1] In section, the nematocysts were found to be about 10 microns long and 4 microns wide and the thread was about at the limit of visibility with an ordinary light microscope. Thus a thread in the scallop mantle cannot be distinguished with the histological technique used. The scallop mantle did, however, show evidence of an inflammatory response (personal communication, Clyde Dawe, National Institutes of Health, Bethesda, Md.). This response was indicated by the greatly increased number of cells under the epithelial margin. Dawe considered these to be wandering amoebocytes coming to the site of the insult.

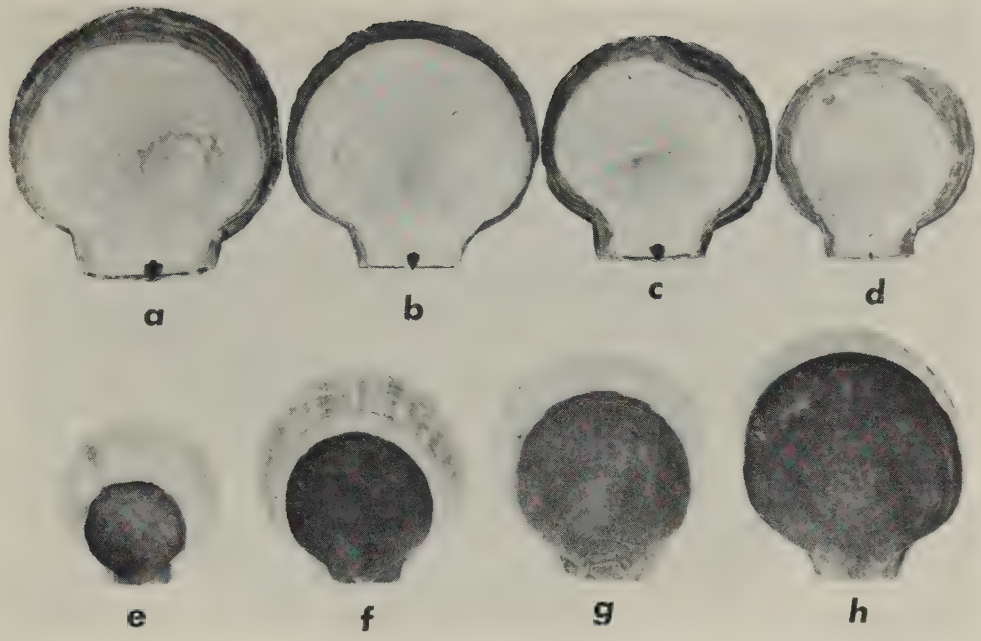

FIGURE 1.—Interior and exterior views of a group of upper (left) valves of *Placopecten magellanicus* showing shell malformation resulting from inner shell invasion by *Hydractinia echinata.* Interior views (a–d) illustrate the persistence of the invading hydroid which causes the scallop to retire further within the shell. External views (e–h) show several scallops that have managed to pass over and grow beyond the hydroids.

thin, slightly irregular, concentric margins secreted by the mantle. Each margin represents successive retreats of the mantle edge.

To resume a normal existence the scallop must successfully overgrow the impinging hydroid colony (fig. 1, e–h). Each time the mantle extends towards the margin it secretes conchiolin, and over this foundation the mantle attempts to produce a new edge of shell over the fringe of the hydroid colony. If it succeeds, shell growth resumes once more. Figure 1b shows an edge of new shell which indicates a successful bridging by the scallop.

A pigment is usually produced in the outer shell layer of the left (upper) valve of the sea scallop. Under some conditions, such as a serious break at the edge of the shell, a scallop secretes new shell material quickly, omitting pigment production until a repair is made and growth becomes normal. The reduction or lack of pigment in scallops as they grow a new lip (fig. 1, e–h) indicates faster rate of shell deposition than usual.

Sometimes a scallop is forced to produce a new edge over the hydroid more than once. Figure 2 shows a scallop that had grown several new shell margins. This is an extreme example but it does illustrate the result of difficulties that sometimes confront scallops. A young scallop increases the periphery of its shell faster than an older one (fig. 1, e) and thus has a better chance to stay ahead of the advancing hydroid.

Hydractinia echinata does not always occupy the entire external shell surface; other epizoons compete for this space as well. Most colonial epizoons live to the severe exclusion of others; it is unusual to see one colony overgrowing another. Usually a distinct zone of demarcation is formed. This also occurs when two colonies of *Hydractinia echinata* meet on the same surface (Schijfsma, 1939). I have examined hundreds of colonies of *Hydractinia echinata* but only once did I find another colonial species growing over the hydroid. This was a granular, encrusting type of unidentified bryozoan spread over the older part of a well-established colony of hydroids. Never was a

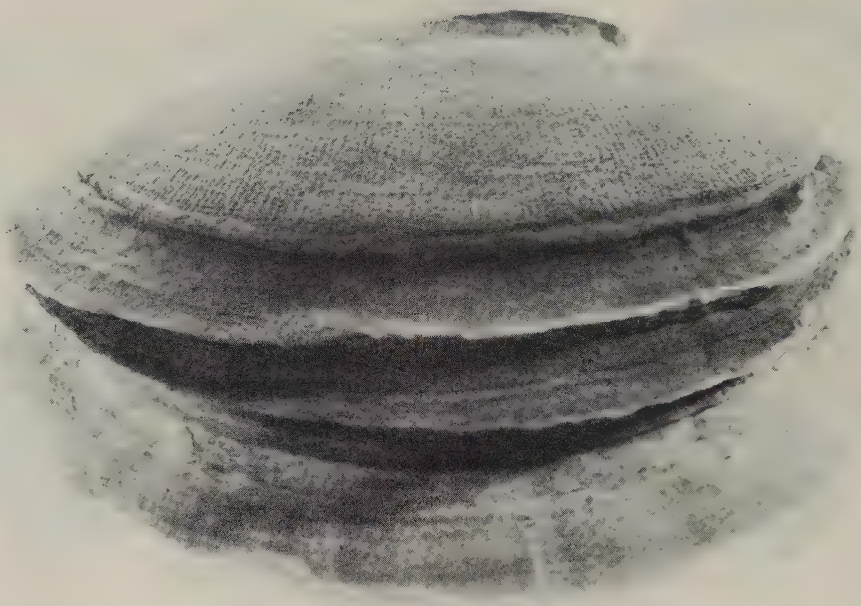

FIGURE 2.—Exterior view of a scallop showing the result when a hydroid colony grows faster than the scallop at successive periods and repeatedly overgrows the shell perimeter.

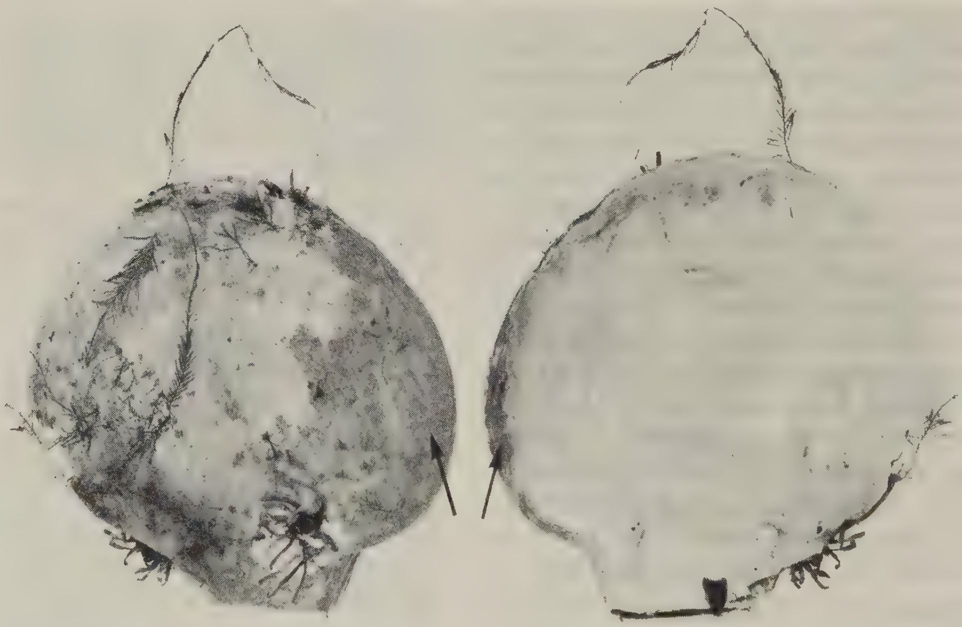

FIGURE 3.—Exterior and interior view of the upper (left) valve of a scallop showing the hydroid partially covering and overgrowing the anterior part of the shell (arrows) causing the scallop to change its shape as it grows in a direction away from the hydroid. (Most fouling organisms were cleaned from the shell before the photo was taken; only chitinous growths remain, including the colonial hydroid, worm tubing, and filamentous hydroids.)

colony of *Hydractinia echinata* seen expanding over another colonial species.

Because of competition with other epizoons, the hydroid often can occupy only a relatively small area of scallop shell surface, hence can inhibit scallop growth over only a relatively small area of the mantle periphery. Limited invasion along the anterior or posterior edge of the shell results frequently in a change in symmetry of the growing scallop; the shell tends to grow more rapidly in a direction away from the disturbed region. Figure 3 shows the interior and exterior view of a scallop shell on which a hydroid that overgrew a short segment of the edge produced a shift in the growth axis. (Note the excavations and deterioration of the shell caused by boring annelids.)

In several instances, expanding colonies of hydroids extended up the plates of barnacles which were also attached to scallop shells. Were they simply seeking additional substrate or did the water currents, created by the feeding barnacles, attract them? Schijfsma (1939) concluded that water currents influence the direction of growth of the colony. Certainly water currents created by a scallop effectively direct growth of a colony toward the shell periphery. Numerous scallops were seen on which the hydroid colony, with equal opportunity to expand in any direction, grew towards the periphery, even obliquely crossing growth lines on the shell in the process.

EFFECTS OF THE ASSOCIATION

Natural mortality of sea scallops, as determined by the ratio of clapper[2] shells to live shells, was uncommonly high in 1960–62 on parts of the important commercial grounds of Georges Bank, off Cape Cod, Mass. (Merrill and Posgay, 1964). We were naturally concerned with the possibility that the hydroid might be responsible for part of this mortality; therefore, during research cruises to Georges Bank in August and September 1961, frequency estimates of *Placopecten magellanicus* and *Hydractinia echinata* were made at all stations where the two species occurred together. Also samples of quick-frozen material from areas of high natural mortality and from areas of high hydroid occurrence were taken to the laboratory for further analyses.

A summary of the results of the analyses is shown in table 1. Samples 1 and 2 are from areas of high hydroid-scallop frequency as reflected by the numbers of hydroids on live and clapper scallops. Samples 3 and 4 are from areas of high clapper–live shell ratios and show a much lower incidence of hydroids. These data make it obvious that the incidence of hydroids and clappers in the same population of sea scallops is not necessarily correlated.

TABLE 1.—*Incidence of occurrence of* Hydractinia echinata *on live and clapper shells of* Placopecten magellanicus

[Samples taken during M/V Delaware cruises 61–13 and 61–16]

Date	Sample number	Location		Number of scallops without hydroids		Number of scallops with hydroids	
		Latitude W.	Longitude N.	Live	Clapper	Live	Clapper
1961				*No.*	*No.*	*No.*	*No.*
Aug. 15	1	41°54.0′	66°39.8′	634	4	208	25
Sept. 24	2	41°53.0′	66°45.9′	300	0	272	16
Aug. 18	3	42°06.1′	66°40.1′	1,123	515	2	1
Sept. 25	4	41°47.1′	66°22.4′	341	42	30	12

Still more apparent is the lack of correlation in the distribution of *Hydractinia echinata* and clappers (fig. 4). As indicated by the darkened area on the chart in Figure 4, areas of high clapper concentration (clapper ratios over 10 percent) in 1961 generally rimmed the

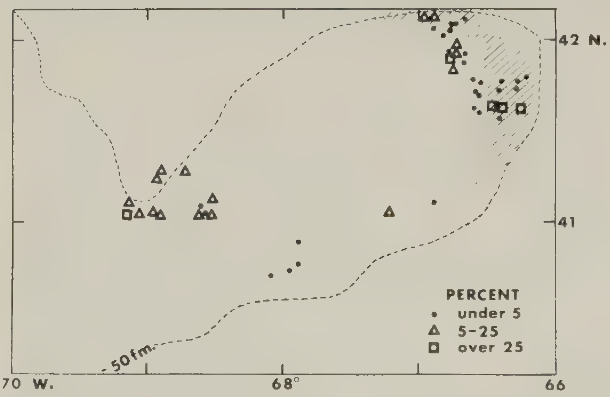

FIGURE 4.—Chart of Georges Bank showing the distribution and density of *Hydractinia echinata* on *Placopecten magellanicus* (symbols) at Georges Bank in relation to the area encompassing high natural mortality in the sea scallop in 1961 (darkened area). Percentage of hydroids on sea scallops indicated.

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[2] The ligament (resilium) holds together the upper and lower valves of a scallop for a period of time after the scallop dies. In this state the shell is referred to as a "clapper."

perimeter from the northern to the lower eastern part of Georges Bank, mostly in depths of 40 to 50 fathoms (73 to 92 m.). Hydroids on scallops in this area, however, were distributed in a more or less straight line from the northern to the eastern part. Furthermore, a high incidence of scallop-hydroid association was found in the western part of Georges Bank where natural mortality was relatively low (fig. 4).

In summary, it can be stated that *Hydractinia echinata* inhibits the sea scallop, but no proof has been found that the hydroid causes the death of scallops.

ASSOCIATION OF *HYDRACTINIA ECHINATA* AND OTHER MOLLUSKS

One colony of hydroids was found partially covering the shell of a 10–mm. pelecypod, *Anomia aculeata* Gmelin, that was attached to the shell of the sea scallop. Careful dissection of the perisarc in this area revealed the shell remains of two other *A. aculeata*, both less than 2 mm. in diameter, completely covered by the colony. *Anomia* attaches to a surface by a partly calcified byssal plug that passes through the bottom shell valve. After the animal dies and the soft parts decompose, the valves soon separate and wash away. As the two valves of both animals were still intact, it appears that the young *Anomia* may have been completely enveloped and smothered by the invader. This circumstantial evidence suggests that mortality of a pelecypod can be attributed to *Hydractinia echinata*.

Gastropod shells also may be occupied by *Hydractinia echinata*. Dead shells of *Nassarius trivittatus* (Say), *Lunatia heros* (Say), *Buccinum undatum* Linnaeus, *Acirsa costulata* (Mighels and Adams), *Colus pygmaea* (Gould), and *Epitonium greenlandicus* (Perry) dredged from the Northern Edge of Georges Bank were covered with *Hydractinia echinata*. The shell apertures were badly deformed, greatly enlarged, and globose. A survey of a large assortment of *Nassarius trivittatus* in the mollusk collection of the Museum of Comparative Zoology at Harvard University revealed several other specimens almost identical to the disfigured ones described above. Apparently this phenomenon is not particularly unusual in nature. Until recently I believed that these deformities of gastropod shell apertures were due to adverse relation between gastropods and hydroids (Merrill, 1964). Further field observations and literature research show, however, that I was wrong. The hydroid grows out on the mouth of the shell only after the snail is dead and only when a pagurid crab inhabits the shell. The deformed and enlarged portion of the shell is made of two layers, the lower by glands of the pagurid, the upper by the hydroid (Aurivillius, 1891). This, then, is a symbiotic association. Enlarging the domain is advantageous to both animals.

One other interesting observation was made regarding the association of *Nassarius trivittatus* and *Hydractinia echinata*. In one dredge haul during R/V *DELAWARE* Cruise 62–7 (station 27, south of Nantucket (lat. 41°11′ N.; long. 70°16′ W.) on June 16, 1962, in 15 fathoms (27 m.)) many live specimens of *Buccinum undatum* were taken. Most of the specimens had colonies of *Hydractinia echinata*. On top of some of the colonies, *N. trivittatus* had deposited masses of egg cases. Evidently the organs necessary for locomotion and egg laying in gastropods are not as sensitive as the mantle in pelecypods to the defensive elements of the hydroid.

CONCLUSIONS AND SUMMARY

Hydractinia echinata frequently lives as an epizoon on the shell of the sea scallop, *Placopecten magellanicus*. It often expands over and around the margin of the shell and interferes with the normal mantle activity of the host. This interference in turn affects normal metabolism and can cause shell malformation. Mortality possibly attributable to this hydroid was noted in a pelecypod, *Anomia aculeata*, as was deformity of many gastropod shells. Thus, *Hydractinia echinata*, which normally uses a shell only as a substrate, is capable of becoming a harmful epizoon.

Geographic distribution of scallops in areas of known high natural mortality and areas of high hydroid occurrence were analyzed to determine the possibility that the hydroid is an epizootic agent. A lack of correlation indicated that the hydroid was not the cause of the heavy natural mortality of scallops.

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OFFSHORE DISTRIBUTION OF *HYDRACTINIA ECHINATA*

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ABSTRACT

New distributional records for this hydroid are listed from 81 offshore locations along the Middle Atlantic region and from Georges Bank, off Massachusetts. The species was commonly found living on the shells of animals having some degree of mobility—sea scallops (*Placopecten magellanicus*), and gastropod shells inhabited by pagurid crabs. The bottom substrate for these animals is predominantly gravelly—a mixture of sand, pebble, and shell. Depths at sampling stations ranged from 16 to 80 fathoms; depths where the hydroid occurred ranged from 16 to 62 fathoms. Deeper stations had soft substrates containing silt and clay, unsuitable for semimotile animals and lacking the hard substrate necessary for hydroid colonization.

Hydractinia echinata (Fleming) is circumpolar in its principal distribution (Fraser, 1946). Fraser (1944) documented the distribution of this hydroid in the western Atlantic, mostly in shoal waters from Salmon Bay, Labrador, to Charleston Harbor, S.C. He recorded numerous locations around the New England coast but none from Georges Bank, although he did include a locality from Georges Basin, near Georges Bank. Only a few scattered and inshore localities were listed for the great Middle Atlantic region. Deevey (1950) extended the range to the Gulf of Mexico.

The purpose of this paper is to describe the bathymetric distribution of *Hydractinia echinata.* Eighty-one new locations on Georges Bank, off Massachusetts, and on the continental shelf of the middle Atlantic bight from depths of 16 to 62 fathoms (fig. 1), complement Fraser's (1944) records from Cape Cod northward. I acquired these data while on research cruises relating to the sea scallop, *Placopecten magellanicus* (Gmelin) (Merrill, 1962; Merrill and Posgay, 1964). This paper is part of a general study to evaluate the significance of an adverse effect of this hydroid epizoon on the commercially important sea scallop (Merrill, 1967).

The hydroid was found colonizing the shells of live sea scallops and the shells of gastropods occupied by pagurid crabs. The scallops and crabs are mobile and inhabit hard rather than soft bottom. Generally, the substrates of stations shallower than 60 fathoms were predominantly sand, pebble, and shell, whereas those deeper than 60 fathoms contained much silt and clay. Depths of the sampling stations ranged from 16 to 80 fathoms. The deepest record for the hydroid was 62 fathoms, which coincided with the greatest depth at which scallops and crabs were taken.

Data on the bathymetric range of *Hydractinia echinata* are sparse. Verrill (1885) stated it was common from low water to 60 fathoms. Smith and Harger's (1874) greatest depth was 65 fathoms. Fraser (1944, 1946) reported the following deepwater locations: 42°02′15″ N., 70°15′ N. [sic], Cape Cod Bay, 362 fathoms; 42°03′ N., 70°37′ W., 30 miles off Cape Cod light, 106 fathoms; 52°01′ N., 68°00′30″ W., off Cape Cod, 86 fathoms. The first two positions are shoal waters, under 25 fathoms. Furthermore, Cape Cod has no water 362 fathoms deep, nor has the whole Gulf of Maine. His third location in 86 fathoms is possible.

A few records from Georges Bank have been noted in the literature. Smith and Harger (1874) listed *Hydractinia polyclina* (= *Hydractinia echinata*) from five stations on the Bank near Cultivator Shoal, the Northern

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Edge, and Corsair Canyon.

The stations on Georges Bank (fig. 1) were made during M/V *Delaware* cruise 61–16, September 22-30, 1961, where *Hydractinia echinata* was found on the shell of *Placopecten magellanicus* (Merrill and Posgay, 1964) in depths from 77 to 136 m. The stations covered most of Georges Bank except the northwest part where few scallops are taken.

Several other locations on Georges Bank where hydroids and sea scallops have been found associated are on figure 1. The records are mostly the result of miscellaneous samples brought to the laboratory.

I looked for *Hydractinia echinata* on gastropod shells inhabited by hermit crabs during a cruise (M/V *Delaware* cruise 60–7) along the middle Atlantic from Block Island to Cape Hatteras, mostly in depths of 20 to 80 fathoms, May 11-21, 1960. The purpose of the cruise was to determine the distribution of sea scallops and other invertebrates. Pertinent information regarding the cruise was given by Merrill (1962). Stations where gastropod shells and hydroids occurred together are plotted in figure 1. The hydroids were found in depths from 16 to 40 fathoms on shells of *Nassarius trivittatus* (Say), *Lunatia triseriata* (Say), *Lunatia heros* (Say), *Colus pygmaeus* (Gould), *Colus stimpsoni* (Mörch), and *Bucci-*

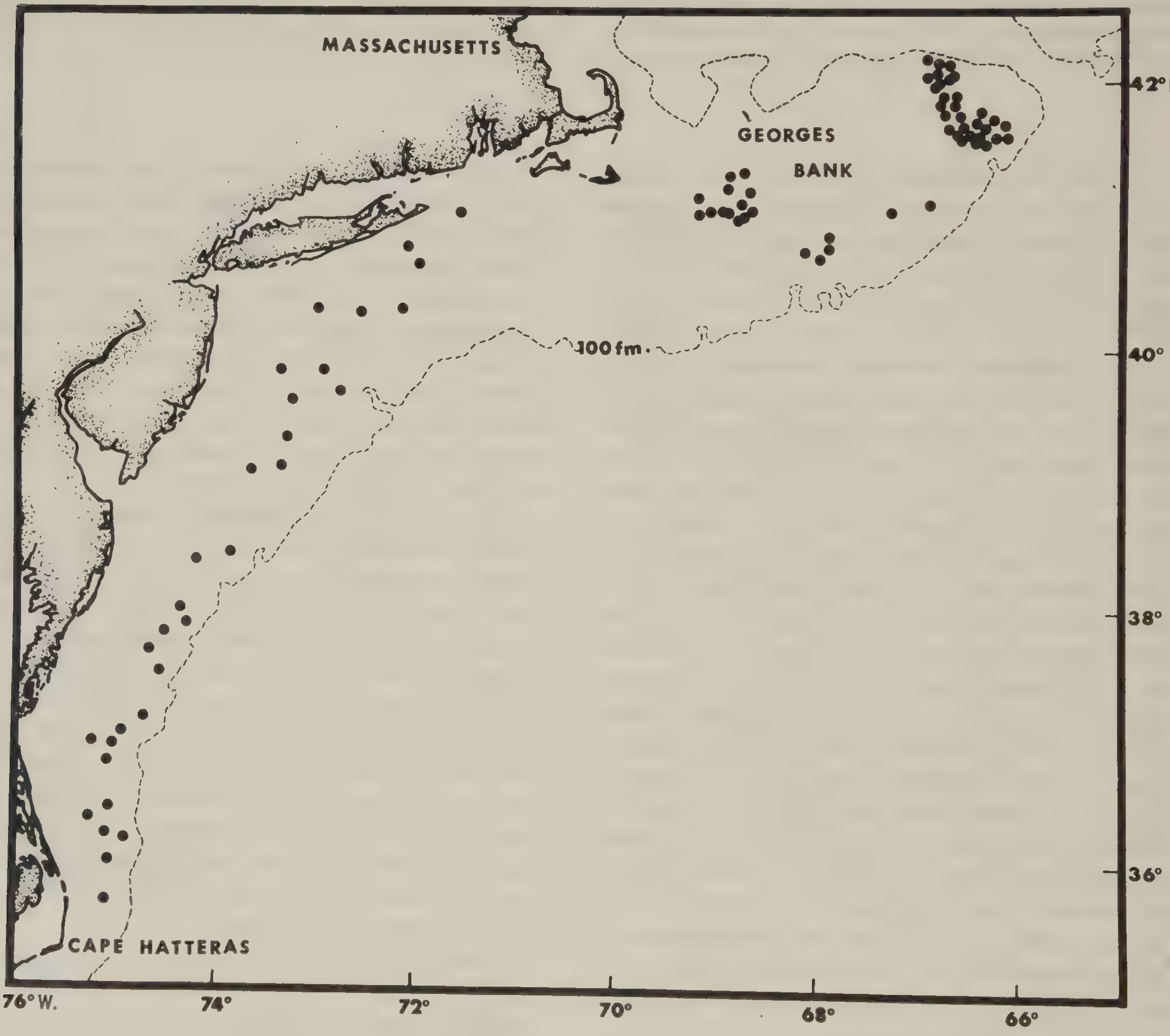

FIGURE 1.—Distribution of the hydroid, *Hydractinia echinata*, in the Georges Bank and middle Atlantic areas. Circles represent locations where the hyroid was taken.

num undatum Linné which were occupied either by *Pagurus bernhardus acadianus* (Benedict) or by *Pagurus pollicaris* (Say).[1]

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[1] Pagurids identified by Anthony J. Provenzano, Jr., University of Miami, Miami, Fla.

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CYCLOPOID COPEPODS OF THE GENUS *TUCCA* (TUCCIDAE), PARASITIC ON DIODONTID AND TETRAODONTID FISHES

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ABSTRACT

The female of *Tucca impressus* Krøyer is redescribed, on the basis of specimens taken from *Chilomycterus schoepfi* (Walbaum) in the Gulf of Mexico. Both genus *Tucca* Krøyer and family Tuccidae Vervoort are redefined, and the genus is treated as monotypic. A restudy of the specimens in the U.S. National Museum revealed that *T. corpulentus* Wilson should be synonymized with *T. impressus* and that the males of *T. impressus* described by Wilson (1911) are actually some immature adult females of the same species before complete metamorphosis.

Metamorphosis occurs only in the cephalothorax and the last two segments of the metasome; the second pedigerous segment and the urosome remain unchanged. The metamorphosis is widening rather than lengthening in the head, but more lengthening than widening in the trunk.

Some geographical variation in size and shape is observed in the metamorphosed parts of the body. The three recognized geographical types are: Atlantic type (with slightly bilobed lateral wings of head and less prominent posterior lobes in trunk), Gulf type (with unlobed lateral wings of head and less prominent posterior lobes in trunk), and Caribbean type (with prominent bilobed lateral wings of head and posterior lobes in trunk). This variation is not strictly expressed, however, by every individual in a given geographical range.

This study was developed from the identification of two specimens of immature adult females of *Tucca impressus* Krøyer, which were collected from the caudal fin of a spiny boxfish, *Chilomycterus schoepfi* (Walbaum), at Alligator Harbor, Fla. The specimens were collected by Jack Rudloe and sent to William A. Newman, Museum of Comparative Zoology, Harvard University, for identification, and subsequently were passed to me through Arthur G. Humes, Department of Biology, Boston University, in May 1965. Because my observations on these two parasites were so different from the description by Wilson (1911), five more collections were obtained and studied. In addition, I reexamined the specimens in the USNM (U. S. National Museum) which were studied by Wilson. This reexamination revealed that Wilson (1911) had introduced errors into our knowledge of the species of the genus *Tucca* Krøyer. The later establishment of a subfamily (by Vervoort, 1962) and family (by Yamaguti, 1963) to contain *Tucca* is based on the information supplied by Wilson.

A redescription of the species and redefinition of the genus and the family are given here. Observations on metamorphosis and geographical variation in morphology are also included.

The redescription of the female of *T. impressus* given below is mainly based on specimens collected off Cape San Blas, in the Gulf of Mexico, because this collection is the largest of my collections, contains numerous females in various stages of growth, and indicates a certain pattern of metamorphosis. The data given in tables 2, 3, and 4 were prepared from this collection to aid in the explanation of metamorphosis.

After the discovery of a certain degree of geographical variation of *T. impressus,* tables 5 and 6 were prepared from the two largest collections in the USNM, one from North Carolina and the other from Jamaica. Table 4 gives data on the specimens taken from the Gulf of Mexico, which also helps to explain geographical variation.

The specimens were dissected and examined in lactic acid, and the figures were drawn with the aid of a camera lucida.

Published May 1967.

SYSTEMATIC ACCOUNT

FAMILY TUCCIDAE VERVOORT, 1962

Diagnosis

Female. — Metamorphosed cyclopoid. Body composed of head, neck, trunk, and "tail." Head formed by fusion of cephalosome and first pedigerous segment, globular dorsally, flattened and hollowed ventrally, and winged laterally. Cephalic appendages and first leg housed in ventral concavity. Neck short, wider than long, formed by second pedigerous segment, distinctly separated from trunk posteriorly. Trunk composed of fused third and fourth pedigerous segments, inflated, much wider than head and neck. "Tail" composed of transformed urosome with all segments completely fused, flattened, wider than long, attached posteroventrally to trunk. Caudal rami small. Eggs multiserate; egg sacs elongate, cylindrical.

First antenna 5- or 6-segmented, with numerous setae. Second antenna 3-segmented; terminal segment armed, in addition to claws and setae, with pectinate, lamelliform process at tip and several rows of teeth or scales over posterior surface. Labrum with marginal teeth; labium weakly developed. Mandible elongate, with two denticulated spines. Paragnath present. First maxilla a small, rounded protrusion, bearing four setae. Second maxilla 2-segmented, tipped with three denticulated spines. Maxilliped indistinctly 3-segmented, terminal segment strongly bent and pointed. Four pairs of biramous legs; rami with reduced segments. Leg five, 1-segmented, segment very small, tipped with three setae. Leg 6 absent.

Male.—Unknown.

Remarks

This family contains but a single genus, *Tucca* Krøyer, 1837. The genus *Tuccopsis* Pearse, 1952, which was included in the family by Yamaguti (1963), is synonymous with *Blias* Krøyer, 1864, of the family Chondracanthidae. This synonymy was first pointed out by Causey (1955: 7) and followed by Vervoort (1962: 93).

When Vervoort (1962) reviewed the family Bomolochidae, he included the genus *Tucca,* following Wilson's (1911) opinion, but he set the genus in a new subfamily Tuccinae. Since Vervoort did not himself examine specimens of the genus *Tucca,* his accounts on the Tuccinae Vervoort, *Tucca* Krøyer, *T. impressus* Krøyer, *T. corpulentus* Wilson, and *T. verrucosus* Wilson were wholly based on Wilson's inaccurate observations (see Remarks in the following two sections). Yamaguti's (1963) account was also based entirely on Wilson's descriptions. Therefore, neither the diagnosis of the family Tuccidae given by Yamaguti (1963: 42) nor the diagnosis of the subfamily Tuccinae given by Vervoort (1962: 92) can be adopted here. The status of the family is then: a redefined family Tuccidae Yamaguti, 1963, embracing within it the redefined and promoted subfamily Tuccinae Vervoort, 1962.

Wilson (1911: 353) pointed out that the copepods of the genus *Tucca* are closely related to the bomolochid copepods, a relationship especially suggested by the mouth parts and other cephalic appendages. I consider the following characteristics of the female of the genus *Tucca,* however, so different from those of the bomolochids that *Tucca* should be placed in a different family:

1. The female undergoes metamorphosis after the last copepodid stage. All known bomolochids (this means all the copepods attributed to the subfamily Bomolochinae by Vervoort in 1962) have no metamorphosis, and all have a cyclopoid form of body. In the tuccids, however, a metamorphosed adult female has its body distinctly separated into head, neck, and "tail;" the appearance is not at all cyclopoid.
2. The urosome of the female is rudimentary, its length less than one tenth of the body. The urosome of the bomolochids is always at least one third as long as the body and distinctly 5-segmented; it comprises a fifth pedigerous segment, a genital segment, and three postgenital segments. Tuccids have a rudimentary fifth pedigerous segment, a genital segment, and a single postgenital segment, all fused into one unit and unsegmented.
3. The fifth leg is very rudimentary, merely a small, single segment armed with three setae. The fifth leg of a typical bomolochid is 2-segmented and consists of a small intermediate

segment and a large spatulate, terminal segment; even in those with a 1-segmented fifth leg, such as the species of *Pseudoeucanthus* Brian and *Orbitacolax* Shen, the free segment is still well developed and spatulate. The terminal, spatulate segment of the bomolochids is usually armed with one spine on the outer surface and two spines and one seta at the distal end.

GENUS *TUCCA* KRØYER, 1837

Diagnosis

Type species is *Tucca impressus* Krøyer, 1837.

Female.—Body form and mouth parts as defined for the family. Eggs multiserate; egg sacs cylindrical, longer than body. First antenna 5– or indistinctly 6–segmented, basal segment armed with a strong hook on ventral surface. Second antenna 3–segmented, bearing terminally five weak claws, three setae, and one pectinate, lamelliform process; distal segment covered with teeth posteriorly. Leg 1 biramous, flattened, and 3–segmented, located on posterior wall of ventral concavity in head. Leg 2 biramous, 2–segmented. Leg 3 and leg 4 with 2–segmented exopod and 1–segmented endopod; intercoxal plate missing. Leg 5 very small, a single segment tipped with three setae. Leg 6 absent.

Male.—Unknown.

Remarks

When Krøyer (1837) established this genus, he gave almost no account of the appendages, and neither did Nordmann (1864) in his description of West African specimens that he called *T. impressus*. Consequently, lacking such information, these authors were inconsistent in the familial attribution of the genus *Tucca*. Krøyer placed it in the family Dichelestiidae and Nordmann in the famliy Chondracanthidae. Both Milne-Edwards (1840) and Bassett-Smith (1899) followed Krøyer's opinion.

The nature of the mouth parts of *Tucca* was not known until 1911, when Wilson studied the specimens of *Tucca* in the collections of the U.S. National Museum. According to his observations, he placed the genus in the subfamily Bomolochinae of the family Ergasilidae, but later, in 1932, he promoted the subfamily to the familial level.

Wilson's additional information on the morphology of the species of *Tucca* was, however, correct only in the gross anatomy of the mouth parts and not entirely right in the fine structures of the mouth parts and other appendages. I discovered these errors after restudying the specimens of *Tucca* that had been studied by Wilson in 1911 (the collections from Woods Hole, Mass., and Beaufort, N.C.), in 1913 (the collections from Montego Bay, Jamaica), and in 1932 (the collections from Woods Hole, Mass.). The new species, *Tucca corpulentus*, described by him, is only a deformed specimen of *T. impressus;* and some immature adult females of *T. impressus* were mistaken by him for adult males. As Vervoort (1962: 93–96) and Yamaguti (1963: 43–44) were misled by Wilson's inaccurate observations, their accounts of the species of the genus *Tucca* should be used with reservations. This problem is discussed in more detail in a later section.

The specimens described by Nordmann (1864: 491–494, pl. VI, figs. 7–10) as *T. impressus* were claimed by Wilson (1911: 359–360) to be a new species, to which he gave the name *T. verrucosus*. I refrain from making any decision on the validity of *T. verrucosus* without consulting either the original material studied by Nordmann or other specimens collected from the same locality (west coast of Africa) and the same host (*Diodon* sp.). If Wilson's assumption is correct, then *T. verrucosus* would naturally be the second species of the genus; however, I now prefer to treat the genus as monotypic.

A doubtful form, *Tucca* sp., was introduced to the genus by Pearse (1952: 12, figs. 23–27). This species, however, has been questioned by Causey (1955: 11) as being probably a mutilated specimen of *Blias prionoti* Krøyer, 1864. The mandible of Pearse's *Tucca* sp. is very convincing evidence that it is not a tuccid. Its form of a "slightly curved hook" indicates a chondracanthid type of mandible rather than a tuccid type.

TUCCA IMPRESSUS KRØYER, 1837

Tucca impressus Krøyer, 1837, pp. 479–482, pl. V, fig. 2 (a–h). Milne-Edwards, 1840, p. 496. Bassett-Smith, 1899, p, 469. Wilson, 1908, p.

625; 1911, pp. 354–387, pl. 48, figs. 102–108, pl. 49, figs. 109–115, 118–120; 1913, p. 200; 1932, pp. 379–380, fig. 243 (a,b). Bere, 1936, p. 582. Heegaard, 1947, pl. 25, fig. 195. Sewell, 1949, p. 157. Carvalho, 1951, p. 136. Pearse, 1952, p. 191. Causey, 1955, p. 3. Vervoort, 1962, pp. 93–95. Yamaguti, 1963, p. 43, pl. 47, figs. 1 (a–k).

Tucca corpulentus Wilson, 1911, pp. 358–359, pl. 49, figs. 116, 117, pl. 50, figs. 121–127; 1932, pp. 380–381, fig. 235 (a,b). Heegaard, 1947, pl. 25, fig. 194. Sewell, 1949, p. 157. Veervoort, 1962, pp. 95–96. Yamaguti, 1963, p. 43, pl. 46, fig. 1 (a–g).

Material Examined

Two immature adult females from caudal fins of 2 *Chilomycterus schoepfi,* caught in mullet seine, at Alligator Harbor, Fla., March 1965; 7 ovigerous females, 3 immature adult females, and 1 copepodid from fins of three *C. schoepfi,* caught in gill net, at Panacea, Fla., May 14, 1965; 44 ovigerous females, 9 immature adult females, and 2 copepodids taken from 14 *C. schoepfi,* caught in shrimp trawl, off Cape San Blas, Fla., May 16, 1965; 6 ovigerous females on dorsal and pectoral fins of 2 *C. schoepfi,* caught in shrimp trawl, off Carrabelle, Fla., July 18, 1965; 9 ovigerous females from fins and body surface of *C. schoepfi,* caught in shrimp trawl by R/V *Oregon,* off St. Simons Island, Ga., November 17, 1965.

In addition to the above collections, I examined the following 16 collections in the USNM (the host names for USNM 38619, 38628, 47748, and 74375 are here changed from *C. geometricus* to *C. schoepfi*):

6090—3 adult females "from exterior surface of rough swellfish, P. Stewart's pound," Woods Hole, Mass., July 26, 1882.

38369—3 adult females and 3 immature adult females from fins of *C. schoepfi,* collected in Louisiana by M. H. Spaulding, August 10, 1907.

38625—8 adult females and 3 immature adult females from fins of *C. schoepfi,* collected at Beaufort, N.C., in 1904.

38627—8 adult females from pectoral fins of *C. schoepfi,* collected at Beaufort, N.C., in 1905.

38628—11 adult females from pectoral fins of *C. schoepfi,* collected at Beaufort, N.C., in 1902.

42251—7 adult females from fins of *C. antennatus* (Cuvier), collected at Montego Bay, Jamaica, June 22, 1910.

42264—5 adult females from pectoral fins of *Diodon hystrix* Linnaeus, collected at Montego Bay, Jamaica, June 22, 1910.

42265—2 immature adult females from pectoral fins of *Spheroides marmoratus* (Ranzani), collected at Montego Bay, Jamaica, June 20, 1910.

42269—1 deformed immature female on fin of *S. marmoratus,* collected at Montego Bay, Jamaica, September 15, 1910.

42273—57 adult females, 1 immature adult female, and 1 copepodid from fins of *C. antennatus,* collected at Montego Bay, Jamaica, June 15, 1910.

47748—19 adult females from *C. schoepfi,* collected at Morehead City, N.C., April 7, 1891.

53525—5 adult females from Beaufort, N.C. (no host or date given).

74375—7 adult females on fins of *C. schoepfi,* collected at Beaufort, N.C., August 1905.

79089—2 adult females under pectoral fin of *C. spinosus* (Linnaeus), collected at Lemon Bay, Fla., in 1934–35.

The following two collections from USNM are labeled as *Tucca corpulentus:*

38619—"Type," 2 adult females (1 decapitated) from fins of *C. schoepfi,* collected at Woods Hole, Mass., in 1887 (see Remarks).

79595—3 adult females on gill of *S. maculatus* (Bloch and Schneider), collected at Woods Hole, Mass., by G. A. Maccallum (no date given; see Remarks).

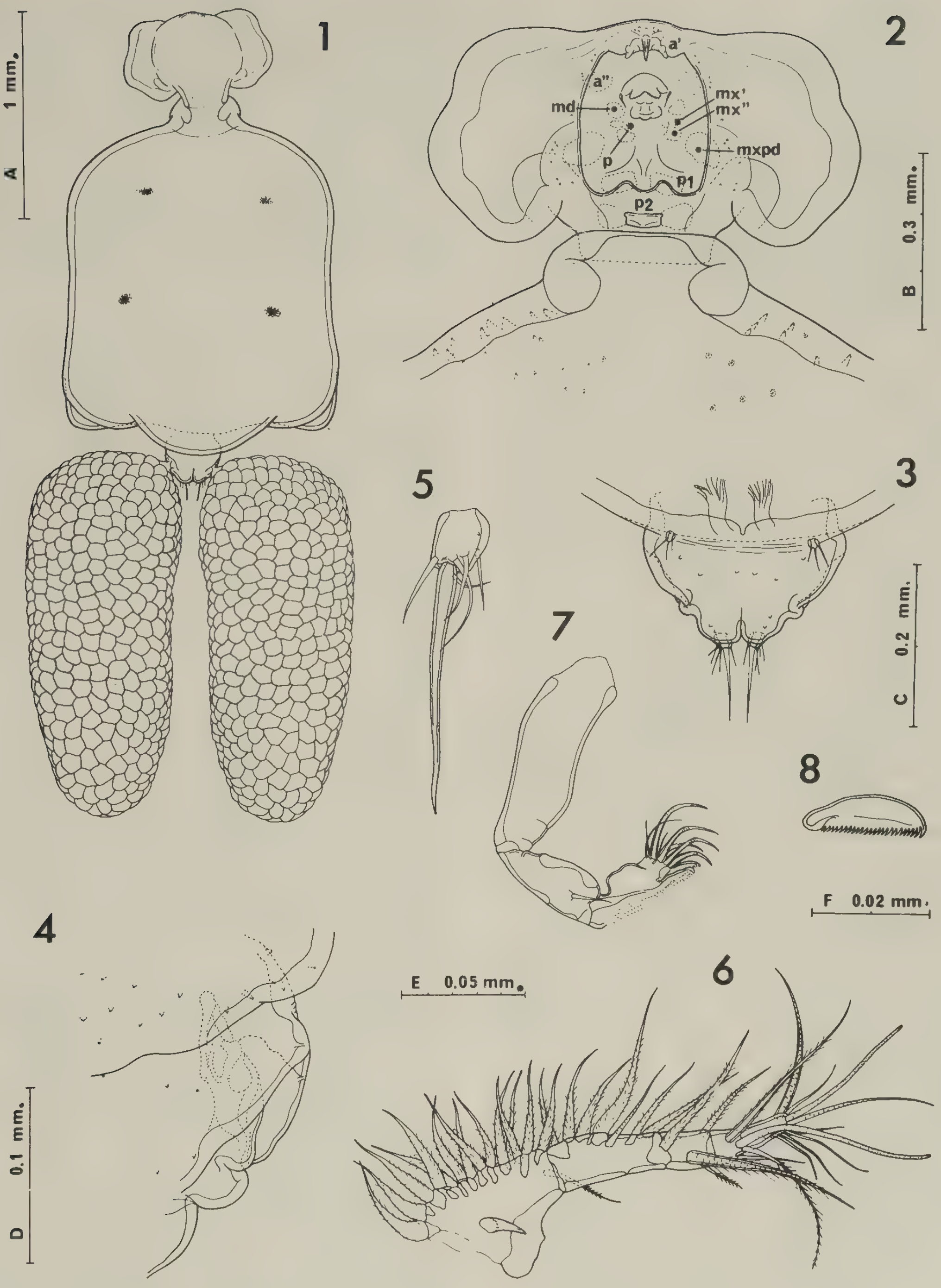
Distribution

See table 1.

TABLE 1.—*Hosts and distribution of* Tucca impressus [1]

Host	Locality	Collection of	Authority
Family Tetraodontidae			
Spheroides maculatus.	Woods Hole, Mass	USNM 6090	Wilson (?)
S. marmoratus	Montego Bay, Jamaica	USNM 42265	Do. (1913)
		USNM 42269	Do. (1913)
Family Diodontidae			
Diodon hystrix	Danish West Indies	?	Krøyer (1837)
	Montego Bay, Jamaica	USNM 42264	Wilson (1913)
Chilomycterus antennatus.	Montego Bay, Jamaica	USNM 42251	Do. (1913)
		USNM 42273	Do. (1913)
C. schoepfi	Woods Hole, Mass	USNM 38619	Do. (1911)
	Beaufort, N.C.	USNM 38625	Do. (1911)
		USNM 38627	Do. (1911)
		USNM 38628	Do. (1911)
	Louisiana	USNM 38369	Do. (?)
	Morehead City, N.C	USNM 47748	Do. (?)
	Beaufort, N.C	USNM 74375	Do. (?)
	Sao Paulo, Brazil	?	Carvalho (1951)
	Alligator Harbor, Fla	?	Pearse (1952)
	Pascagoula, Miss	Author	Causey (1955)
	Panacea, Fla	do	Present paper
	Cape San Blas, Fla	do	Do. paper
	Carrabelle, Fla	do	Do. paper
	St. Simons Island, Ga	do	Do. paper
C. spinosus	Lemon Bay, Fla	USNM 79089	Bere (1936)

[1] Nordmann's record of *Tucca impressus* from the west coast of Africa is excluded, because of its uncertain identification. USNM 53525 is also not included because the host was not identified.



FIGURES 1–8. *Tucca impressus*, female, from *Chilomycterus schoepfi* taken off Cape San Blas, Fla., in the Gulf of Mexico. The letter in the parentheses after the explanation of each figure refers to the scale at which the figure was drawn. 1. Entire, dorsal (A). 2. Head, neck, and anterior end of trunk, showing relative position of various cephalic appendages, ventral (B). 3. "Tail" (= urosome), ventral (C). 4. Genital segment, showing egg sac attachment area, dorsal (D). 5. Caudal ramus, ventral (E). 6. First antenna, exterior (E). 7. Second antenna, exterior (E). 8. Lamelliform process at tip of second antenna, interior (F). (a'.=first antenna; a".=second antenna; md.=mandible; mx'.=first maxilla; mx".=second maxilla; mxpd.=maxilliped; p.=paragnath; p_1.=leg 1; p_2.=leg 2).

Description of Stages

Three stages are described below: mature ovigerous female, immature adult female, and female copepodid.

Mature ovigerous female: — Body (fig. 1) noncyclopoid, 1.51 to 2.92 mm. long, composed of head, neck, trunk, and "tail." Head (fig. 2) small, 0.46 by 0.71 mm., representing a fusion of cephalosome and first pedigerous segment; inflated dorsally, flattened ventrally (fig. 25), and with two wide lobed wings laterally, which in a fully grown adult female protrude beyond anterior margin of cephalosome. Ventral surface of head deeply invaginated at center, forming a hollow disk (fig. 2) which is reinforced anteriorly by rostrum and bases on first antennae and posteriorly by flattened leg 1. Second antennae, mouth parts, and maxillipeds found on bottom of this disk. Rostrum (fig. 2) well developed, bearing some refractile points, two sclerotic protrusions, and one fairly strong hook pointing posteroventrally.

Head jointed to trunk by a short neck (fig. 2) which is formed by second pedigerous segment; this segment completely fused with head anteriorly. This portion of body highly variable in length in different individuals, fully extended in some specimens and completely contracted in others, leaving practically no space between head and trunk. Trunk (fig. 1) made up of third and fourth pedigerous segments, 1.54 by 1.31 mm., nearly square, with rounded corners. Posterior corners slightly produced on each side into one dorsal and one ventral lobe (fig. 25), and a third lobe produced from posteromedial end of trunk between two dorsal lobes. Four depressions (fig. 1) on dorsal surface of trunk. "Tail" (fig. 3) flattened, 0.17 by 0.26 mm., attached to trunk posteroventrally (fig. 25), totally or partially concealed by dorsal posteromedial lobe. No appreciable segmentation seen in "tail," which apparently represents a fusion of the narrow fifth pedigerous segment, the circular genital segment, and one small postgenital segment. Egg sac attachment area (fig. 4) well developed, occupying about two-thirds of lateral surface of "tail." Caudal ramus (fig. 5) small, 23 by 20 μ, armed with five short setules and one long seta 114 μ long. Egg sac elongate, cylindrical; fully grown sac longer than body, containing numerous small eggs with a diameter of 90 μ. Many micropits on surfaces of head and trunk, as shown in detail in figs. 2 and 4, penetrating deeply into sclerotic covering of body.

First antenna (fig. 6) distinctly 5-segmented, but second segment suggesting a division into two segments. Armature on these five segments, from proximal to distal: 15 + 1 hook (on ventral surface), 8, 3, 3, + 1 aesthete, and 7 + 1 aesthete.

Second antenna (fig. 7) 3-segmented; basal segment longest, naked; second segment bearing one seta. Terminal segment having subterminally a rod-shaped process and one pectinate, lamelliform process (fig. 8), and carrying terminally three setae and five weak claws; several rows of teeth on posterior surface.

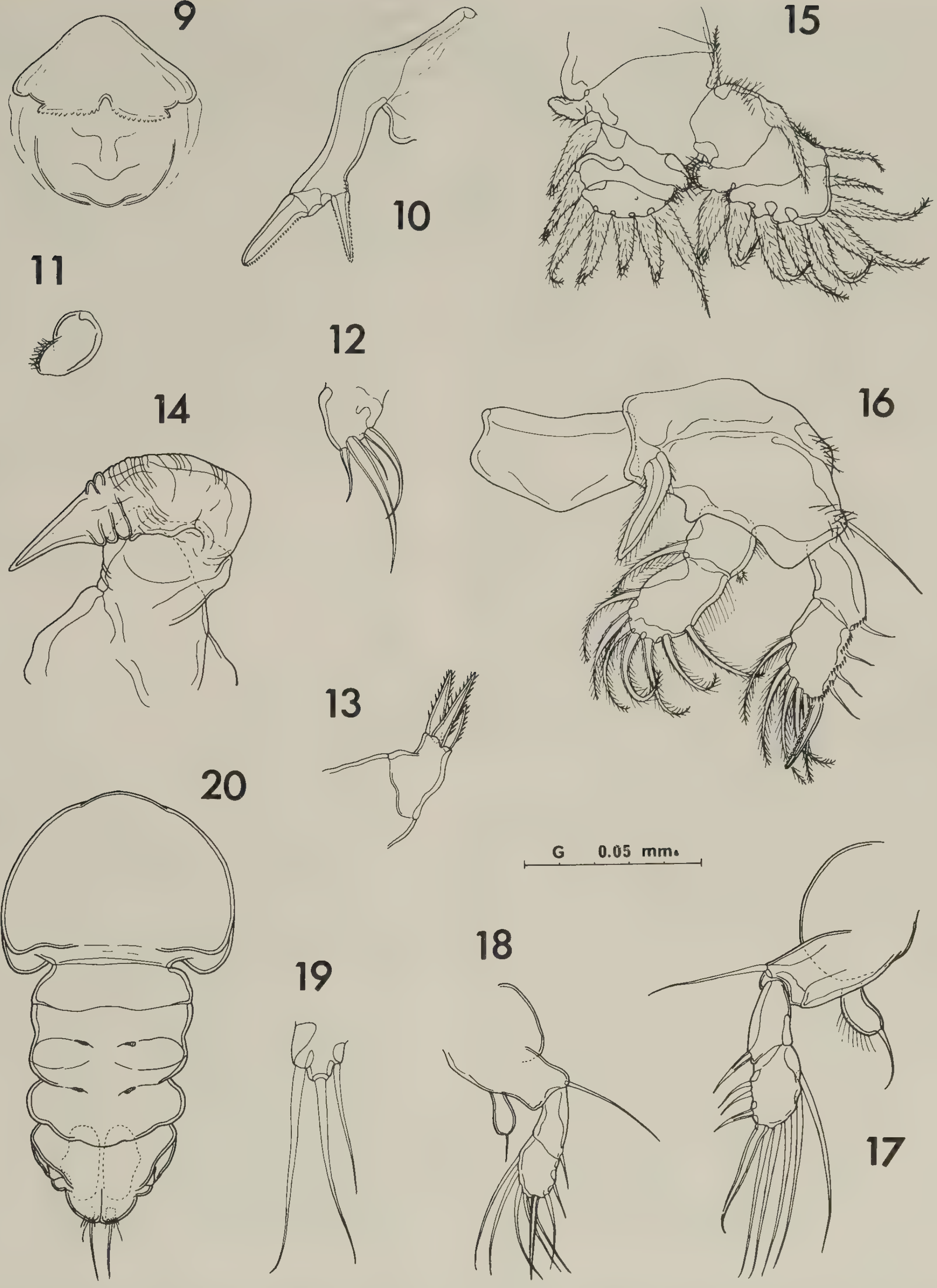
Labrum (fig. 9) well developed, with fine teeth on posterior free margin; labium weak. Mandible (fig. 10) composed of a large plate produced into long process, armed with one terminal masticatory process and one subterminal, bilaterally denticulated spine. Paragnath (fig. 11) bearing setules, located posteromedially to mandible. First maxilla (fig. 12) a small rounded protrusion, located laterally to paragnath, bearing four setae, one of which is fairly long. Second maxilla (fig. 13) 2-segmented, terminal segment armed with three bilaterally denticulated spines.

Maxilliped (fig. 14) powerfully developed, indistinctly 3-segmented; terminal segment strongly bent inward and almost perpendicular to first two segments. Last segment sharply pointed, with well-developed sclerites cutting into ventral and posterior surfaces, thus making these surfaces corrugated. In many specimens, the terminal, pointed process, broken when the parasite was removed from the host, appeared as a blunt process.

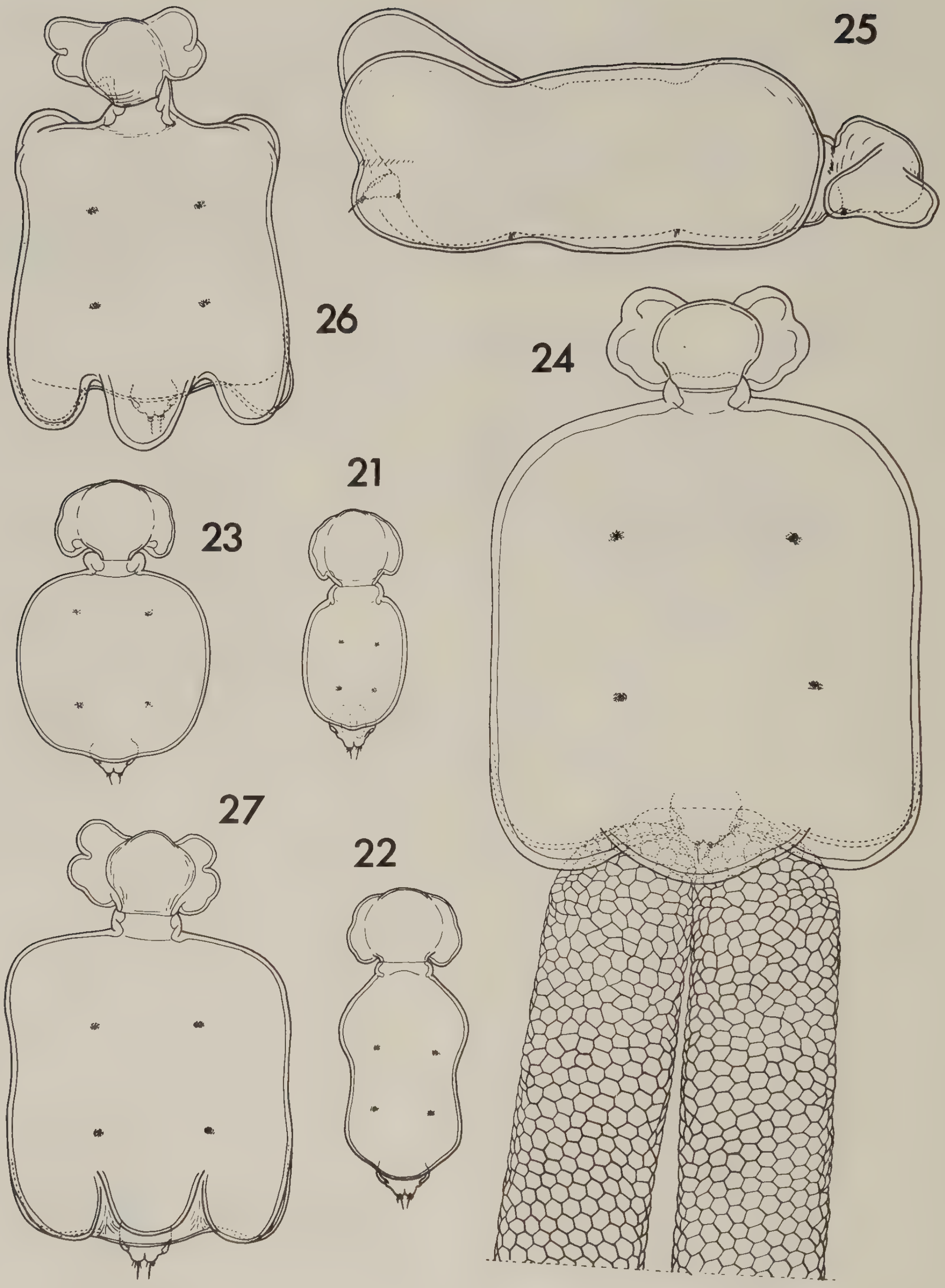
Formula of spines and setae on first four pairs of legs as follows (Arabic numerals represent setae and Roman numerals spines):

	Protopod	Exopod	Endopod
Leg 1	0-0 1-0	1-0 1-1 7	0-1 0-1 5
Leg 2	0-0 1-I	1-0 III-I-5	0-1 7
Leg 3	0-0 1-0	I-0 III-I-5	1
Leg 4	0-0 1-0	I-0 II-I-5	1

Leg 1 (fig. 15) strongly flattened, its setae



FIGURES 9–20.—*Tucca impressus*, female, from *Chilomycterus schoepfi* taken off Cape San Blas, Fla. in the Gulf of Mexico. 9. Labrum and labium, ventral (G). 10. Mandible, posterior (G). 11. Paragnath, ventral (G). 12. First maxilla, anterior (G). 13. Second maxilla, anterior (G). 14. Maxilliped, posteroventral (D). 15. Leg 1, anterior (D). 16. Leg 2 and intercoxal plate, anterior (E). 17. Leg 3, anterior (G). 18. Leg 4, anterior (G). 19. Leg 5, ventral (F). 20. Copepodid, dorsal (B).



FIGURES 21-27.—*Tucca impressus,* female. Figures 21–23, from *Chilomycterus schoepfi* taken off Cape San Blas, in the Gulf of Mexico; 24–25, from *C. schoepfi* taken off St. Simons Island, Ga.; 26–27, from *C. antennatus* at Montego Bay, Jamaica. 21. Immature adult with short trunk, dorsal (A). 22. Immature adult with guitar-shaped trunk, dorsal (A). 23. Immature adult with circular trunk, dorsal (A). 24. Entire, dorsal (A). 25. Same, lateral (egg sacs omitted) (A). 26. Entire, dorsal (egg sacs omitted) (A). 27. Entire, showing absence of anterior lobes in trunk (egg sacs omitted) (A).

densely haired. Medial surface of basis produced into blunt process, covered with hairs; marginal surfaces of every segment in each ramus also covered with hairs. Spines on outer surfaces of exopods of leg 2 (fig. 16), leg 3 (fig. 17), and leg 4 (fig. 18) weakly developed, setiform, and naked. Intercoxal plate absent in leg 1, leg 3, and leg 4; coxa and basis not completely separated in leg 3 and leg 4. Leg 5 (fig. 19) uniramous, very rudimentary, 10 by 9 μ; located at junction of "tail" and trunk and armed with three long setae. Leg 6 absent.

Immature adult female.—Body (figs. 21-23) noncyclopid, shaped differently in different stages of metamorphosis; proportions of various body regions also different in different stages (see table 2).

Table 2.—*Measurements of immature adult females taken from* Chilomycterus schoepfi *off Cape San Blas, Fla., in the Gulf of Mexico.*

Specimen number	Head	Neck	Trunk	"Tail"	Total length
	Mm.	*Mm.*	*Mm.*	*Mm.*	*Mm.*
1	0.28 by 0.44	0.08	0.47 by 0.47	0.17 by 0.24	0.96
2	.36 by 0.49	.09	.45 by 0.49	.17 by 0.23	1.07
3	.34 by 0.49	.10	.51 by 0.57	.17 by 0.27	1.12
4	.31 by 0.49	.10	.74 by 0.56	.17 by 0.25	1.13
5	.33 by 0.52	.10	.70 by 0.54	.18 by 0.24	1.23
6	.30 by 0.47	.11	.82 by 0.60	.17 by 0.23	1.31
7	.34 by 0.55	.10	.73 by 0.56	.18 by 0.23	1.33
8	.34 by 0.57	.09	.75 by 0.60	.17 by 0.26	1.35
9	.31 by 0.56	.11	.85 by 0.86	.16 by 0.25	1.43
Average	0.32 by 0.51	0.10	0.67 by 0.64	0.17 by 0.25	1.21

Structure of appendages similar to mature ovigerous female. Details of these immature adult females are given in following section in discussion of metamorphosis.

Female copepodid.—Body (fig. 20) cyclopoid, 0.70 by 0.37 mm. (excluding setae on caudal rami); no segmentation on cephalothorax and urosome, but with clear distinction between each two adjoining regions of four body regions. Cephalothorax semicircular anteriorly and rather truncated posteriorly; posterior surface roughly separated into dorsal and ventral portions. Second pedigerous segment (= neck of adult), 0.08 by 0.26 mm., attached to center of posterior surface of cephalothorax, carrying leg 2 ventrally at anterior margin. Third pedigerous segment, 0.13 by 0.26 mm., slightly invaginated on both sides and incompletely separated from fourth pedigerous segment on dorsal surface. Fourth pedigerous segment, 0.12 by 0.26 mm., with posterior margin protruding over about one-third of urosome. Urosome (= "tail" of adult) 0.17 by 0.23 mm., carrying inside a pair of seminal receptacles (or cement glands ?). Egg sac attachment area similar to that in adult.

Caudal ramus attached to posteroventral surface of urosome, its armature as in adult. Two sclerites on dorsal surface of third and fourth pedigerous segment. Micropits present on body surface (omitted in fig. 20).

All appendages similar to those in adult ovigerous female and immature adult female.

Remarks

In the vial labeled Cat. No. 38619 in the collection of USNM are two specimens (one decapitated) designated by Wilson (1911) as the type specimens of *Tucca corpulentus*. The trunk of the headless specimen appears like the one shown in fig. 24, namely, squarish and distinctly 3-lobed on its posterodorsal surface. The head of this specimen was supposedly dissected by Wilson for study of the mouth parts and other cephalic appendages, and probably was the source of his figs. 122–125. The other specimen (with head) is, doubtlessly, the source of his fig. 121. I have examined the latter specimen with great care in lactic acid. Nevertheless, I was not able to find any appendages that are significantly different from those described above. In addition, the posterodorsal surface of the trunk is also 3–lobed, not as smooth as illustrated by Wilson in his fig. 121. The circular appearance of this specimen is possibly due to the fact that the parasite was somewhat pressed (by the fin, on which the parasite was attached, pressing against the body surface) before preservation, because its trunk appears unusually thin. The absence of pits or impressions on body surface, one of the characters cited by Wilson for establishing the new species, is conceivably also due to mechanical deformation prior to preservation.

Consequently, as far as these two type specimens are concerned, *T. corpulentus* does not differ from *T. impressus* and should be synonymized with it. There are some inconsistencies between the label of Cat. No. 38619 in the USNM and the statement of Wilson (1911: 359): "There is but a single lot of this species, which was taken from the northern swell–toad, *Spheroides maculatus,* at Woods Hole, Massachusetts, and is numbered 38619, U.S.N.M. It includes three females, two of which bear egg–strings." The label of Cat. No. 38619 clearly says, however, that there are only "2 ♀ specimens," the host is "*Chilomycterus geometricus,*" and no egg strings were found in the vial. Another USNM collection of *T. corpulentus* is Cat. No. 79595. The label of this collection fits better with Wilson's statement. It says that there are "3 specimens" and the host is "Gills, *Spheroides maculatus,*" but the three specimens of this collection are *Pseudochondracanthus diceraus* Wilson. They are mature adult females and all carry a pygmy male on their posteroventral surface. This collection was not mentioned by Wilson in any of his reports, not even in his reports of *P. diceraus* (1908: 436; 1932: 496), but the label says "Identified by C. B. Wilson." I have taken the two specimens kept in the vial of Cat. No. 38619 as Wilson's type specimens of *T. corpulentus* and synonymized the species with *T. impressus.*

One of the three immature adult females in the vial of Cat. No. 38625 was obviously mistaken by Wilson for an adult male. The rather small size, the different shape and proportion of various body regions, and the two bean-shaped reproductive organs inside the urosome might suggest incorrectly a male, if the process of metamorphosis in the female is unknown. The pair of stout hooks described by Wilson on the ventral surface at the posterior corners of the genital segment of this "male" specimen are merely two sclerotic protrusions (see fig. 3).

NOTES ON METAMORPHOSIS

The absence of the male parasites on the diodontid and tetraodontid fishes perhaps occurs because males do not grow beyond the copepodid stage. They probably die after copulation as do the males in the families Lernaeidae, Lernaeoceridae, and Pennellidae, in which only the female copepodid (after copulation) attaches to the fish host and metamorphoses into an adult.

The two youngest females recovered from the diodontid fish caught off Cape San Blas, Fla., still show a cyclopoid form of body; they are particularly reminiscent of bomolochid and taeniacanthid copepods (see fig. 20). The cephalothorax is the widest part of the body, and the metasomal segments are still distinguishable (see table 3 for measurements). These features, in comparison with the metamorphosed adult female, indicate that they are either still in the last copepodid stage or, at most, just on the way to metamorphosis. The somewhat older females that I have in the same collection are the nine copepods that show no segmentation in the metasomal region, have swollen trunks as wide as the head or a little wider, and carry no egg sacs (see figs. 21, 22). These females I have considered as the immature adults inasmuch as they have attained sexual maturity and have copulated but have not yet produced egg sacs.

TABLE 3.—*Measurements of female copepodid from three collections.*

Record and body part measured	Specimen 1	Specimen 2	Specimen 3	Specimen 4
Host	*Mm. Chilomycterus schoepfi*	*Mm. Chilomycterus schoepfi*	*Mm. Chilomycterus schoepfi*	*Mm. Chilomycterus antennatus*
Locality	Panacea, Fla.	Cape San Blas, Fla.	Cape San Blas, Fla.	Montego Bay, Jamaica
Date	May 14, 1965	May 16, 1965	May 16, 1965	June 15, 1910
Cephalothorax (head)	0.27 by 0.37	0.31 by 0.41	0.30 by 0.42	0.31 by 0.47
Thorax (neck +trunk)	.30 by 0.26	.34 by 0.32	.36 by 0.31	.41 by 0.37
Urosome ("tail")	.17 by 0.23	.16 by 0.23	.17 by 0.21	.15 by 0.23
Total length	.70	.81	.83	.86

Metamorphosis occurs only in the cephalothorax and the last two segments of the metasome. As far as the size and shape are concerned, the second pedigerous segment and the urosome in the copepodid are not significantly different from the neck and the "tail" in the immature adult female, nor in the ovigerous female. The second thoracic segment, urosome, and all appendages are not transformed during metamorphosis, but the cephalothorax and the third and fourth pedigerous segment are tremendously changed.

The size of the head of an immature adult female (0.32 by 0.51 mm.) is not much different from that of the cephalothorax in the copepodid (0.31 by 0.42 mm.); the shape, however, is markedly different. The expansion is seen mostly in anterior corners, posterior subcorners, and the dorsal surface of the head. The head of an ovigerous female (0.33 by 0.59 mm.) differs from that of the immature adult female chiefly in the more globular appearance of the middorsal surface; it is not lengthened but definitely widened. The metamorphosis in the head involves changes in form from semicircular to rectangular (in dorsal view) and from slightly convex to globular (in lateral view of the dorsal surface). The amount of increase in proportions of the head is about 10 percent in the length and 45 percent in the width; this widening rather then lengthening during metamorphosis is due to the formation of the lateral wings.

The second and third pedigerous segments are completely fused into a unit at the onset of metamorphosis (fig. 21). This fused trunk is then enlarged in three dimensions, the shape (in dorsal view) changes from oval (as in fig. 21) to guitar-shaped (as in fig. 22) or nearly circular (as in fig. 23) and then to squarish (as in fig. 1). The posterior lobes, three on the dorsal and two on the ventral surface, are not formed in the immature adult female. The four chitinized platelets on the dorsal surface of the thorax of the copepodid are retained throughout metamorphosis. As these platelets are the points of attachment of trunk muscles on the tergum of the second and third pedigerous segment, they have not been elevated by the enlarging action in the course of metamorphosis. Thus, the four platelets form the bottom of the "four pits" on the dorsal surface of the ovigerous female. The amount of increase in proportions of the trunk is about 270 percent in the length and 120 percent in the width. The metamorphosis of the trunk, contrary to that of the head, involves more lengthening than widening.

Specimens 4, 5, 6, 7, and 8 of table 2 have trunks distinctly longer than wide; they look like that in fig. 22. The remaining four specimens (1, 2, 3, and 9) of the immature adult females in the same collection have trunks nearly as long as wide and resemble fig. 23. In the present state of knowledge, we can say only that immature adult females have two forms. Which form comes first in the process of metamorphosis is unknown.

A comparison between table 2 and table 4 shows that the maturity of the females can be judged by the size of the trunk, in addition to the presence or absence of egg sacs. The trunk is definitely longer and wider in ovigerous females than in immature adults, although the size of the head overlaps broadly in the two stages.

The first ovigerous female in table 4 has smaller body length, but a definitely larger trunk, than the largest immature adult female in table 2. As noted in the previous section, the neck of this ovigerous female is unusually shrunken; therefore, body length alone is not a good measure for determining the maturity of a female.

GEOGRAPHICAL VARIATION

According to our present knowledge of parasitic copepods of fishes, *Tucca impressus* is parasitic exclusively on two families of fishes, Tetraodontidae and Diodontidae—especially the fishes of the latter family (porcupine fish or boxfish). Our past records show that it is most abundant on the fishes of the genus *Chilomycterus* (Diodontidae) and always found either on the fins or on the body surface.

A certain degree of variation is observed in the head and the trunk of the ovigerous females collected from three different areas, namely the west coast of North Atlantic Ocean, the Gulf of

TABLE 4.—*Measurements of smallest, largest, and eight randomly selected ovigerous females taken from* Chilomycterus schoepfi *off Cape San Blas, Fla., in the Gulf of Mexico*

Specimen number	Head	Neck	Trunk	"Tail"	Egg sac	Total length
	Mm.	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
1	0.29 by 0.50	0.06	1.30 by 0.95	0.17 by 0.24	0.84	1.38
2	.30 by 0.61	.11	1.10 by 1.22	.16 by 0.23	1.29	1.51
3	.33 by 0.55	.09	1.12 by 0.93	.17 by 0.25	.75	1.54
4	.31 by 0.56	.09	1.19 by 1.02	.18 by 0.23	1.10	1.59
5	.31 by 0.64	.09	1.14 by 0.87	.19 by 0.26	broken	1.68
6	.30 by 0.60	.08	1.33 by 1.12	.18 by 0.26	broken	1.71
7	.35 by 0.56	.10	1.30 by 1.40	.18 by 0.25	1.34	1.75
8	.36 by 0.65	.09	1.31 by 1.31	.18 by 0.24	1.84	1.77
9	.38 by 0.59	.11	1.28 by 1.48	.16 by 0.25	broken	1.78
10	.33 by 0.65	.10	1.59 by 1.14	.18 by 0.26	1.41	2.02
Average	0.33 by 0.59	0.09	1.24 by 1.17	0.17 by 0.25		1.67

TABLE 5.—*Measurements of smallest, largest, and eight randomly selected ovigerous females taken from* Chilomycterus schoepfi *at Morehead City, North Carolina (from USNM 47748)*[1]

Specimen number	Head	Neck	Trunk	"Tail"	Egg sac	Total length
	Mm.	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
1	0.38 by 0.67	0.10	1.76 by 1.65	0.18 by 0.24	(2.79)	2.24
2	.30 by 0.78	.09	2.02 by 1.60	.17 by 0.23	-------	2.47
3	.35 by 0.96	.08	2.15 by 2.06	.19 by 0.24	-------	2.63
4	.37 by 0.91	.12	2.30 by 1.79	.16 by 0.25	-------	2.79
5	.31 by 0.84	.13	2.29 by 1.89	.16 by 0.26	-------	2.80
6	.34 by 0.88	.11	2.50 by 1.98	.16 by 0.24	-------	2.90
7	.36 by 0.85	.12	2.39 by 1.95	.17 by 0.27	-------	2.97
8	.37 by 0.91	.09	2.51 by 1.86	.18 by 0.26	-------	2.98
9	.38 by 0.94	.11	2.49 by 2.42	.19 by 0.27	-------	3.09
10	.40 by 0.89	.12	2.46 by 1.95	.17 by 0.25	(4.61)	3.16
Average	0.36 by 0.86	0.11	2.39 by 1.92	0.17 by 0.25	-------	2.80

[1] The egg sacs were found free in the vial. Since there is no way to identify each sac with its female, only the shortest and the longest sacs were measured.

TABLE 6.—*Measurements of smallest, largest, and eight randomly selected ovigerous females taken from* Chilomycterus antennatus *at Montego Bay, Jamaica (from USNM 42273)*

Specimen number	Head	Neck	Trunk	"Tail"	Egg sac	Total length
	Mm.	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
1	0.31 by 0.48	0.11	0.93 by 0.83	0.17 by 0.26	0.68	1.42
2	.32 by 0.54	.09	.96 by 0.78	.19 by 0.27	broken	1.46
3	.33 by 0.60	.09	1.15 by 1.13	.18 by 0.25	1.02	1.59
4	.35 by 0.56	.10	1.29 by 1.10	.16 by 0.27	1.77	1.75
5	.34 by 0.58	.08	1.42 by 1.22	.18 by 0.26	broken	1.78
6	.35 by 0.59	.11	1.35 by 1.29	.16 by 0.23	1.59	1.81
7	.34 by 0.56	.12	1.41 by 1.26	.15 by 0.24	2.05	1.83
8	.33 by 0.66	.09	1.47 by 1.27	.18 by 0.26	2.14	1.95
9	.36 by 0.66	.10	1.46 by 1.36	.18 by 0.25	broken	2.00
10	.34 by 0.68	.11	1.67 by 1.41	.17 by 0.26	broken	2.14
Average	0.34 by 0.59	0.10	1.31 by 1.17	0.17 by 0.26	-------	1.77

Mexico, and the Caribbean Sea. This variation occurs only in the metamorphosed parts of the body, and is in the size and the shape. A comparison of fig. 1 (a representative from the Gulf of Mexico), fig. 24 (a representative from the west coast of North Atlantic Ocean), and fig. 26 (a representative from the Caribbean Sea) together with reference to tables 4, 5, and 6 shows this picture of geographical variation. In the following discussion, for the sake of convenience, the specimens from Georgia, North Carolina, and Massachusetts are termed as the Atlantic type; the specimens from Florida (west coast), Mississippi, and Louisiana, the Gulf type; and the specimens from Jamaica, the Caribbean type.

The bilobed condition of the lateral wings of the head is generally most pronounced in the Caribbean type (figs. 26, 27), but the wings are almost unlobed in the Gulf type (fig. 1). The lateral wing of the Atlantic type (fig. 24) is only slightly bilobed; the posterior lobe is larger than the anterior lobe and is wider than those in the other two geographical types.

In both Gulf type and Atlantic type, the posterior lobes in the trunk are usually less pronounced, and there are no anterior lobes. These anterior and posterior lobes are, however, present and well formed in the Caribbean type. A fully grown ovigerous female of an Atlantic type is much larger than those of the Gulf type and the Caribbean type. The following data were derived by considering all collections from a general geographical region as a whole to show the size ranges (in millimeters) of the ovigerous females of the three different geographical types:

	Caribbean type	Gulf type	Atlantic type
	Mm.	*Mm.*	*Mm.*
Smallest	1.36 (in USNM 42251)	1.51 (off Cape San Blas, Fla.)	1.59 (in USNM 38625)
Largest	2.14 (in USNM 42273)	2.51 (Carrabelle, Fla.)	3.16 (in USNM 47748)
Longest egg sac	2.78	4.09	4.61

Thus, the shape of the trunk indicates that the Gulf type is closer to the Atlantic type than to the Caribbean type, but the size of the trunk indicates that the Gulf type is, on the contrary, closer to the Caribbean type than to the Atlantic type. In other words, comparisons of the trunk show that the Gulf type is intermediate between the Atlantic type and the Caribbean type. The variation of the head, in the Atlantic type, instead of the Gulf type, shows the intermediate character in the bilobed condition of the lateral wings.

I have found specimens in USNM collections (Cat. No. 38625 and 74375), from Beaufort, N.C., which, instead of having the Atlantic type trunk, have the posterior lobes of the trunk fairly well defined as in the Caribbean type. Moreover, in the collections from Jamaica, some individuals lack the anterior lobes in the trunk, as shown in fig. 27. It appears, therefore, that the variation in the head and the trunk is not absolute, or, in other words, that this variation is merely a general tendency of modification that exists in a certain geographical area but is not strictly expressed by every individual of this species found in a given geographical range. As the hosts of this parasitic copepod are mostly inshore fishes and not powerful swimmers, considerable distant movement probably is accomplished only by drifting with the current. At present, however, it is impossible to determine whether the Gulf Stream has influenced this picture of geographical variation.

The single specimen of *T. impressus* described by Krøyer (1837) is a female taken from the inner surface of the pectoral fin of a *Diodon hystrix* in the Danish West Indies. It definitely belongs to the Caribbean type, since in Krøyer's fig. 2a (dorsal view) and fig. 2b (lateral view) the posterior lobes, anterior lobes, and the bilobed condition in the head are of that type. According to Krøyer's description (p. 479) this Danish West Indian specimen measures 2 lines, of which the egg sac is about half. In other words, the length of the parasite's body is about 2.11 mm., which falls within the range of the Caribbean type (see table 6).

The 37 specimens of *T. impressus* described by Carvalho (1951) from Brazilian *C. schoepfi* measure from 1.52 to 1.80 mm., and so fall within the range of the Caribbean type.

In his discussion of the validity of Nordmann's *T. impressus,* Wilson (1911: 359) expressed his doubt upon the variation of the specimens of *T. impressus:* "either Nordmann's species or that of the present author is new to science. They can not both be identical with Krøyer's *T. impressus.*" This implies that Wilson's specimens are different from Krøyer's *T. impressus* to a certain degree, but this difference is not as significant as the discrepancy between Krøyer's *T. impressus* and Nordmann's *T. impressus.* Consequently, Wilson identified his specimens collected in Beaufort, N.C., as *T. impressus,* and created *T. verrucosus* for Nordmann's *T. impressus.*

The total length (1.67 mm.) given by Wilson (1911: 356) for the species of *T. impressus* is too small for the Atlantic type. I have measured all 30 specimens that were identified by Wilson as *T. impressus* in USNM collections. The collections, number of specimens, and maximum sizes are:

Catalogue number	Number of specimens	Smallest (*mm.*)	Largest (*mm.*)
USNM 38625..	11 (3 immature)	1.13	1.69
USNM 38627..	8	2.04	2.23
USNM 38628..	11	1.86	2.49

It is obvious, therefore, that Wilson took into consideration only the specimens in USNM 38625. This collection unfortunately contains no fully grown ovigerous females (judged by the length of the egg sac). One of the three immature adult females in this collection was described by Wilson as a male, and the measurements given for it are (Wilson, 1911: 357):

Total length, 1.27 mm.; cephalothorax, 0.3 by 0.5 mm.; trunk 0.75 by 0.51 mm.; and width of genital segment, 0.25 mm.

These figures lie within the range of the immature adult female with a longer (guitar-shaped) trunk given in table 2.

The 10 specimens of *T. impressus* reported by Nordmann (1864) were taken from a "fleckigen Diodon-Art." According to Nordmann's description on p. 491, these parasites measure about 5 mm. long including the egg sac. Judging from his illustration of a complete parasite in pl. VI, fig. 7, the body is about 3.15 mm. long and the egg sac, 1.85 mm.; therefore, the size is about that of the Atlantic type of the *T. impressus.* According to what Nordmann described (pp. 491–494) and illustrated (pl. VI, figs. 7–10), however, this West African species of *Tucca* is definitely different from all three types of *T. impressus* in the North and South American waters.

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MORPHOLOGY AND DISTRIBUTION OF LARVAL WAHOO *ACANTHOCYBIUM SOLANDRI* (CUVIER) IN THE CENTRAL PACIFIC OCEAN

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ABSTRACT

Descriptions are presented of the early developmental stages of the wahoo, *Acanthocybium solandri* (Cuvier), ranging from 2.8 to 23.7 mm. in standard length. Developmental changes in body pigmentation, body form, fin formation, and ossification of bones and other hard parts were studied for 38 larvae collected in the central Pacific Ocean. Drawings of larvae at various sizes are included. Certain adult characters are discussed, such as: the number of vertebrae and the vertebral formula; the number of spines and rays in the first dorsal, second dorsal, and anal fins; and the number of dorsal and anal finlets.

Larval and adult wahoo live in the open ocean as well as near land. The adults spawn throughout the tropical and subtropical waters between lat. 30° N. and 25° S. The species spawns throughout the year in the equatorial waters between lat. 14° N. and 15° S., and during the northern and southern summer in areas farther from the Equator.

Although considerable knowledge has been gained in recent years about the early life history of the commercially important mackerels and tunas, the larval and juvenile stages of many scombroid fishes are poorly known. This is particularly true of the larvae of the wahoo, *Acanthocybium solandri* (Cuvier). The smallest wahoo previously recorded was a 23.7–mm. juvenile from the central Pacific Ocean (Strasburg, 1964). Prior to this record, the only mention of a young wahoo in the literature was a 28–cm. juvenile caught off Japan in 1917 (Kishinouye, 1923).

The wahoo, a member of the Scombridae, is usually taken in small quantities as incidental catches on the longline, and in larger quantities by surface trolling (Iversen and Yoshida, 1957). It is found in tropical and subtropical areas of the oceans.

While sampling for tuna larvae in the central Pacific Ocean from 1950 to 1962, the Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii, collected 38 young wahoo from 2.8 to 17.8 mm. SL (standard length) in plankton net hauls. The morphology and distribution of the larvae were studied to increase our knowledge of the early life history of the scombroid fishes.

This paper describes the developmental changes in body pigmentation, fin formation, and ossification of various bones. It also discusses certain adult characters that require definition, such as the number of vertebrae and the vertebral formula, the number of spines and rays in the dorsal and anal fins, and the number of finlets. The growth rates of various body parts are included, as well as new information on distribution of the species in the central Pacific Ocean, as determined from captures of the larvae and adults.

COLLECTION AND TREATMENT OF MATERIAL

Plankton hauls were made with a 1–m. plankton net on 32 cruises of the Bureau of Commercial Fisheries research vessels *Hugh M. Smith* and *Charles H. Gilbert* from May 1950 to July 1962. The types of hauls varied slightly over the years; generally, the net was hauled obliquely from a depth of 200 m. to the surface before 1956, but from 1956 to 1962, it was

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hauled obliquely from 140 m. to the surface. On a few cruises the net was hauled obliquely from a depth of 60 m. and horizontally near the surface. Each haul lasted 30 minutes.

Of the 1,643 plankton samples obtained, 600 were taken near the Hawaiian Islands (lat. 15° to 30° N., long. 150° to 165° W.) and most of the others in the equatorial region (lat. 10° N. to 10° S., long. 110° to 170° W.). The 38 wahoo larvae were found in 34 plankton samples; 2 larvae were found in two samples and 3 larvae in one (fig. 1 and table 1). All the larvae were preserved in a 10 percent solution of Formalin.[1] The wahoo larvae ranged from 2.8 to 17.8 mm. SL. The size range was extended to 23.7 mm. by the inclusion of a juvenile (collected in a midwater trawl) described by Strasburg (1964).

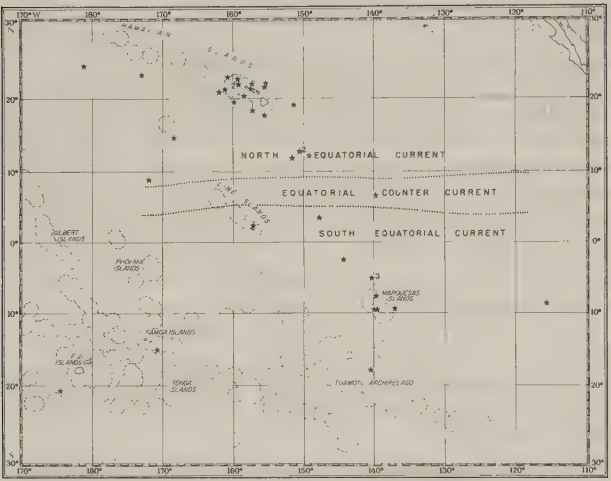

FIGURE 1.—Locations at which wahoo larvae were taken in plankton net hauls. Each star represents a single larva. A star and number show catches of two or more larvae. Broken lines indicate a distance of 110 kilometers from land. Major currents of the central Pacific Ocean are shown.

TABLE 1.—*Record of larval and juvenile wahoo captured in plankton net hauls in the central Pacific Ocean, 1950–62*

Limits of latitude and date	Cruise	Position		Local time	Surface temperature	Distance from land	Standard length
		Lat.	*Long.*		*° C.*	*Km.*	*Mm.*
Lat. 15°–30° N.							
May 17, 1950	HMS-4 [1]	21°06′ N.	161°06′ W.	0925	24.6	139	3.4
May 18, 1950	HMS-4	19°25′ N.	159°50′ W.	1048	24.8	185	4.1
May 24, 1950	HMS-4	21°53′ N.	159°09′ W.	0120	22.8	93	2.8; 4.2
June 17, 1954	HMS-26	20°51′ N.	161°59′ W.	0512	25.9	222	3.1
July 1, 1950	HMS-5	22°58′ N.	173°00′ W.	2312	26.1	333	7.4
July 12, 1962	CHG-58 [1]	22°44′ N.	160°47′ W.	0100	25.5	139	5.8
July 22, 1951	HMS-10	22°27′ N.	159°15′ W.	0715	25.6	37	4.8
July 30, 1951	HMS-10	21°25′ N.	155°30′ W.	1343	25.5	110	4.3
Aug. 5, 1953	HMS-21	21°10′ N.	157°28′ W.	0240	25.4	28	5.5
Aug. 7, 1953	HMS-21	21°53′ N.	155°21′ W.	0315	24.8	157	3.8
Aug. 16. 1960	CHG-48	24°15′ N.	178°54′ E.	1800	26.7	592	8.7
Aug. 19, 1950	HMS-6	20°15′ N.	158°24′ W.	2340	26.7	130	8.4
Aug. 21, 1953	HMS-21	17°40′ N.	155°30′ W.	0120	25.0	130	4.6
Aug. 21, 1953	HMS-21	18°14′ N.	157°09′ W.	2038	25.8	148	4.3
Sept. 10, 1952	HMS-17	21°48′ N.	157°18′ W.	1149	25.2	37	4.4
Oct. 4, 1951	HMS-11	19°00′ N.	151°19′ W.	0750	25.4	389	5.7
Lat. 14° N.–14° S.							
Jan. 12, 1959	HMS-50	12°42′ N.	150°24′ W.	2006	26.1	890	7.6; [2] 7.9
Feb. 9, 1958	HMS-43	7°35′ S.	139°40′ W.	2110	28.5	46	7.8
Mar. 13, 1954	CHG-15	8°42′ S.	115°39′ W.	1954	26.4	2,057	5.8
Mar. 16, 1956	HMS-33	5°03′ S.	140°16′ W.	1949	26.3	315	5.2; 6.2 [2] 6.6
Apr. 16, 1954	CHG-15	2°09′ N.	157°05′ W.	1932	27.7	28	4.3
Apr. 23, 1958	CHG-38	2°34′ S.	144°12′ W.	2003	28.4	732	17.8
Apr. 25, 1958	CHG-38	3°15′ N.	147°40′ W.	2003	28.6	1,047	9.0
May 29, 1952	HMS-15	6°36′ N.	139°44′ W.	1035	27.7	1,556	6.6
June 10, 1954	HMS-26	14°33′ N.	168°25′ W.	1739	26.6	232	10.7
June 19, 1958	HMS-45	12°02′ N.	149°03′ W.	2010	27.0	1,055	5.9
July 6, 1950	HMS-5	8°54′ N.	172°00′ W.	2012	26.9	912	4.5
Aug. 30, 1956	CHG-30	9°22′ S.	137°01′ W.	2000	25.2	167	9.2
Oct. 6, 1957	CHG-35	11°42′ N.	151°30′ W.	0000	27.6	908	5.2
Dec. 1, 1957	CHG-35	9°33′ S.	139°51′ W.	0839	27.5	56	10.2
Dec. 1, 1957	CHG-35	9°34′ S.	139°50′ W.	1406	28.6	56	3.9
Lat. 15°–25° S.							
Feb. 14, 1962	CHG-55	20°34′ S.	175°29′ E.	2004	27.0	145	13.2
Mar. 5, 1957	HMS-38	17°56′ S.	140°28′ W.	2030	28.1	28	2.8
Mar. 13, 1962	CHG-55	15°05′ S.	170°48′ W.	2000	27.9	56	6.8

[1] Bureau of Commercial Fisheries research vessels, *Hugh M. Smith* (HMS) and *Charles H. Gilbert* (CHG).
[2] Length of 7.9-mm. and 6.6-mm. specimens estimated.

Of the 38 larvae, 21 were cleared in a weak (1–2 percent) solution of potassium hydroxide and stained with alizarin in the technique described by Lipman (1935). Standard length and various body parts were measured, and counts of fin rays and spines, myomeres, teeth, and branchiostegal rays were made before clearing and rechecked after staining. Vertebrae were counted after the specimens had been stained. In a few instances where the body was slightly bent, a small piece of glass slide was placed over the specimen to straighten it before measuring. The following measurements were made on each specimen:

Standard length: The distance from anteriormost tip of snout to posterior end of notochord; after the notochord had flexed dorsad, the distance from tip of snout to posterior edge of hypural complex was measured.

Head length: The distance from anteriormost tip of snout to dorsal end of gill cover.

Snout length: The distance from anteriormost tip of premaxillary to anterior edge of orbit.

Orbit diameter: The greatest distance measured along the longitudinal axis of the body.

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[1] Trade names referred to in this publication do not imply endorsement of commercial products.

This measurement was chosen over eye diameter because the eyes tend to shrink in preservative, and some had been lost.

Premaxillary length: The distance from tip to anterior edge of the mesethmoid, measured along the dorsal profile of the snout.

Upper and lower jaw lengths: The distance from anteriormost tip to posterior edge of maxillary and mandible.

Body depth: Vertical distance immediately behind the anus.

Snout to anus distance: The straight-line distance from anteriormost tip of snout to posterior edge of anal opening.

Snout to first and second dorsal fins: the straight-line distance from anteriormost tip of snout to origins of the fins.

DEFINITION OF CERTAIN ADULT CHARACTERS

In the identification of larval and juvenile fishes, it is important that the adult characters be defined accurately because they are often applicable to the young as well. One useful skeletal character for the diagnosis of adult scrombrids is the number of vertebrae. Previous literature on the wahoo contains a wide variation in vertebral number, which is unusual in the family Scombridae. The number of vertebrae among most scombrids is known to be nearly constant (Ford, 1937; Godsil and Byers, 1944; Clothier, 1950), but a number of reports with descriptions of wahoo (table 2) give the vertebral formula as 23 to 33 + 31 to 34 = 54 to 66 (precaudal vertebrae + caudal vertebrae = total vertebrae).

I found that all papers published after 1923 which contained the formula 23 to 33 + 31 to 34 = 54 to 66 included Kishinouye (1923) as a reference. Kishinouye (1908, 1915, 1923) did not, however, discuss the wide range in number of precaudal vertebrae, or refer to the seemingly low count of 23 precaudals. It seems likely that the 23 first reported by Kishinouye (1923) is a typographical error and that 32 is the correct number.

Other evidence supports my suspicion that the reported low count of 23 precaudal verte-

TABLE 2.—*Counts of some meristic characters of wahoo*

Source	Length [1]	First dorsal spines	Second dorsal fin			Anal fin			Vertebrae		
			Rays	Finlets	Total	Rays	Finlets	Total	Precaudal	Caudal	Total
From literature	*Mm.*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
Cuvier and Valenciennes (1831)		26	11	9	20	12	10	22			
Lay and Bennett (1839)		25		9½			9½				
Poey (1860)[2]	1,300 (FL)	25									
Doderlein (1872)[2]		26									
Jordan (1885)		24	I, 12	9	22	I, 12	9	22			
Jenkins (1904)		27	13	9	22	12	8	20			
Jordan and Evermann (1905)		25									
Kishinouye (1908)		26	11	10	21	11	9	20			65
Starks (1910)									32	34	66
Kishinouye (1915)		26	11	9	20	11	9	20	32 or 33	31	63–64
Kishinouye (1923)		26	11	9	20	11	9	20	32–33	31	[3] 63–64
Kishinouye (1923)	1,092 (FL)	26	11	9	20	11	9	20	33	31	[4] 64
Meek and Hildebrand (1923)	1,200 (FL)	26	12	9	21	II, 10	9	21			
Conrad and La Monte (1937)	1,468 (FL)										
Conrad (1938)		26							31	31	62
Morice (1953)		26		[4] 9			[4] 9				64
Strasburg (1964)	23.7 (SL)	27			24			23	32	31	63
Specimens examined by present author											
Longline fishing	1,435 (FL)	27	12	9	21	13	9	22	32	33	65
Do	1,554 (FL)	27	13	9	22	12	9	21	31	32	63
Do	1,252 (FL)	27	12	[5] 9(10)	21	12	[5] 9(10)	21	32	31	63
Do	1,066 (FL)	27	12	[5] 9(10)	21	13	[5] 9(10)	22	32	31	63
Do	1,300 (FL)								32	30	62
Do	1,245 (FL)								32	31	63
Marlin stomach	159 (SL)								32	31	63
Do	152 (SL)								32	31	63
Skipjack stomach	117 (SL)								31	33	64
Plankton haul	17.8 (SL)	27			23			22	33	30	63
Do	13.2 (SL)	27			23			22	32	31	63

[1] FL (fork length); SL (standard length).
[2] From Lütken, 1880.
[3] Number of precaudal and total vertebrae as corrected.
[4] From figure.
[5] Last 2 finlets fused.

brae is erroneous. First, no other report in the literature shows a wahoo having between 23 and 31 precaudal vertebrae, as one would expect if these counts encompassed the actual range of variation; instead, the number of precaudal vertebrae has always been cited as 31, 32, or 33 when it was referable to a particular specimen. Second, I found that six adult wahoo taken during a cruise of the *Charles H. Gilbert* to the southwestern Pacific in 1963 had either 31 or 32 precaudal vertebrae and 30 to 33 caudal vertebrae (table 2). Six juvenile specimens from other sources had 31 to 33 precaudal and 30 to 33 caudal vertebrae.

Although the number of vertebrae may vary slightly more in wahoo than in tunas, the variation is less than Kishinouye (1923) reported. The vertebral formula for wahoo can be restated as 31 to 33 + 30 to 34 = 62 to 66; the most typical formula is 32 + 31 = 63.

Other adult characters that are useful for identifying young wahoo are the number of spines and rays in the dorsal and anal fins. Varying counts have been given for these characters, also. Different authors have reported 24 to 26 first dorsal spines, except Jenkins (1904) who reported 27 (table 2). Each of four adult wahoo that I examined had 27 first dorsal spines, but the last 2 were greatly reduced and were buried beneath the skin and muscle tissue. Although it was relatively easy to locate the 26th spine by probing, it was extremely difficult to locate the 27th even with careful dissection of skin and musculature. This difficulty may account for the generally lower spine counts reported previously for the first dorsal fin. Three juvenile wahoo that I examined, including the specimen previously reported by Strasburg (1964) as having 26 spines, also had 27 first dorsal spines. The last spine was extremely small and appeared almost to be the first spine in the second dorsal fin. The number of spines in the first dorsal fin of the wahoo thus appears to be constant at 27.

The number of rays seems to vary slightly in the second dorsal (12 to 14) and anal fins (12 to 13). The counts of 11 rays for both fins in all of Kishinouye's reports and 11 rays for the second dorsal fin reported in Cuvier and Valenciennes (1831: table 2) may be too low (by error), or may represent extreme variations.

In adult wahoo the dorsal and anal finlets appear to be constant at 9, although Robert H. Gibbs, Jr. (personal communication) found the number to vary between 7 and 9 in 16 specimens he examined. While preparing the skeletal material for the present study, I observed that the posteriormost dorsal finlet and the posteriormost anal finlet, which appeared to be perfectly formed single finlets, were actually composed of two separate finlets that had become fused. The extra finlet is clearly reflected in the total ray and finlet counts of the three smallest wahoo (table 2). In both dorsal and anal series the number of elements is generally larger than the combined ray and finlet number of the adults.

DESCRIPTION AND DEVELOPMENT OF LARVAL AND JUVENILE WAHOO

Identification of wahoo larvae is simplified because it is a single species (Lütken, 1880; Jordan and Evermann, 1905; Beaufort and Chapman, 1951; Collette and Gibbs, 1963) and therefore the problem of differentiating morphologically similar species is eliminated. The larval characteristics described and illustrated in this paper were obtained from specimens that had been preserved in 10 percent Formalin for many years and were sometimes based on single specimens. The description, therefore, may differ slightly from that of newly caught specimens.

Larval wahoo less than 3.4 mm. SL are readily recognized by several characteristics: (1) the large number of body segments in relation to body length; (2) the elongate viscera; and (3) the presence of one or two black pigment spots on the ventral surface of the caudal peduncle, similar to those on larvae of skipjack tuna (*Katsuwonus pelamis*). Larvae as small as 2.8 mm. have 63 to 65 body segments, including the urostyle (compared with 42 to 43 segments in skipjack), and the viscera extend well over one-half the body length. Larvae above 4.4 mm. can be recognized by the large number of body segments, the extent of the viscera (over two-thirds the body length), and the length of the snout (more than twice the diameter of the orbit).

The development of the larval and early juvenile stages is discussed in the following sequence: (a) changes in pigmentation, (b) changes in body form, and (c) sequence of ossification. The term "larva" includes all specimens from the smallest to the juvenile stage, which starts at the time the full complement of spines and rays in all fins has ossified. In wahoo this point is reached before 23.7 mm. SL. The term "postlarva" is not used here. Standard length is the measure of body length, except when specified otherwise.

CHANGES IN PIGMENTATION

As is true for all fish larvae preserved in Formalin, the only pigment spots visible in wahoo larvae are the melanophores. Unlike larvae of *Trachurus* (Ahlstrom and Ball, 1954), Exocoetidae (personal observation), Istiophoridae (Ueyanagi, 1963), *Coryphaena* (Mito, 1960), and others, the wahoo larvae have comparatively few melanophores. Large changes in pigmentation as the larvae increase in size are seen only in four areas: (1) snout, (2) base of second dorsal fin, (3) base of anal fin, and (4) digestive tract (figs. 2 and 3). The following descriptions of pigmentation are based on the left side of the body as seen in lateral view.

Head Pigmentation

The midbrain area remains unpigmented in larvae smaller than 4.4 mm. (fig. 2A and B). The only exception was a 3.1–mm. larva which possessed a melanophore in this location. A single melanophore is present on the anterior portion of the midbrain in about half the larvae between 4.4 and 5.5 mm. (fig. 2A). Pigmentation in the anterior portion of the midbrain increases gradually with body length; 6 melanophores are present in the 10.7-mm. larva (fig. 3C), and about 27 in larvae up to 13.2 mm. long (fig. 3D).

Pigmentation appears on the forebrain much later than on the midbrain and the number of melanophores is small. A single melanophore appears on the forebrain in larvae about 7.4 mm. long, and the number of melanophores increases to only four or five in larvae up to 17.8 mm. long (specimen similar in appearance to that of figure 3D, except for heavier pigmentation).

Lateral pigmentation on the posterior portion of the head is completely lacking in larvae up to 13.2 mm. long, but about 50 small melanophores are present in the area posterior to the orbit and on the surface of the preopercle in larvae about 17.8 mm. long. In larvae of yellowfin tuna (*Thunnus albacares*) and skipjack tuna, some melanophores usually are present in the postorbital region in specimens shorter than 6.0 mm.

Pigmentation on the snout develops in two major areas: near the primordial nasal cavity and on the tip of the upper jaw. It is present on the snout in the smallest larva as a single small melanophore within the primordial nasal cavity and two or three melanophores on the tip of the upper jaw (fig. 2A). The pigmentation at the primordial nasal cavity develops slowly; additional melanophores are added within the cavity and on the surface of the snout anterior to it. As the nostrils form (when the larvae are between 10.7 and 13.2 mm. long), a few more melanophores appear on the surface of the snout between the anterior and posterior nostrils. The number of melanophores in this area is small, however, for no more than 13 to 15 are present in the 13.2-mm. larva (fig. 3D).

The number of melanophores increases slowly on the anterior portion of the upper jaw of larvae up to a length of about 4.3 mm.; however, above this size, as the upper and lower jaws begin to grow more rapidly in relation to body length, pigmentation on the anterior portion of the upper jaw increases noticeably. At a length of 6.8 mm. (fig. 3A), two or three rows of 18 to 25 melanophores are on the anterior part of the upper jaw. The number of melanophores increases with further growth of the fish, and the entire surface of the upper jaw anterior to the mesethmoid is covered in larvae larger than 13.2 mm. (fig. 3B-D). Additional melanophores develop posteriorly on the snout, and in the 17.8–mm. larva the pigmentation on the anterior portion of the upper jaw and around the nostrils has merged into a single, large pigmented area.

The tip of the lower jaw in larvae 2.8 mm. long has few melanophores, but the number

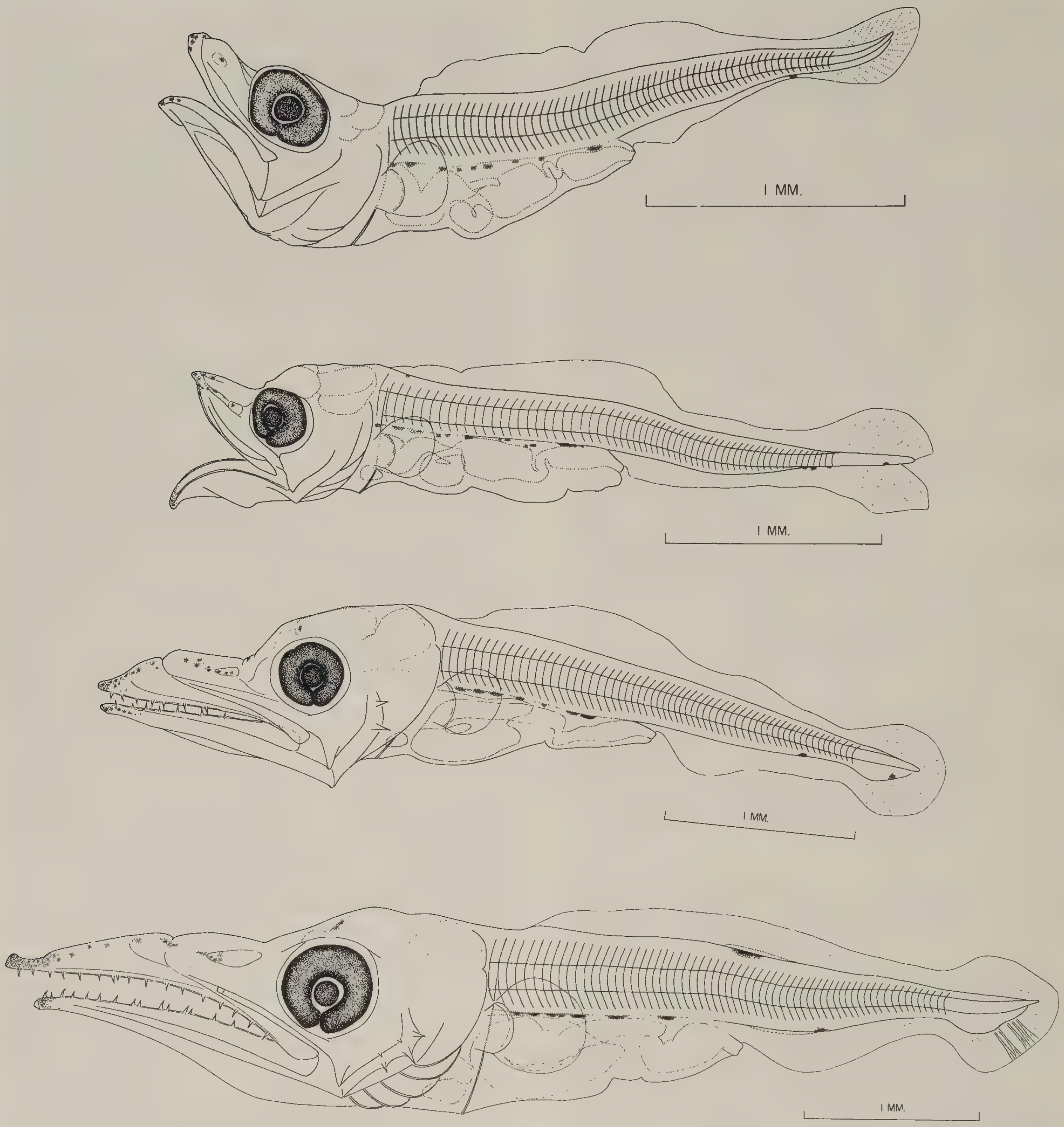

FIGURE 2.—Development of the larva of wahoo: A. larva, 2.8 mm. long; B. larva, 3.4 mm. long; C. larva, 4.4 mm. long; D. larva, 5.8 mm. long.

increases gradually to about seven or eight in the 8.4-mm. larva (fig. 3B). No melanophores appear on the conical cartilaginous projection at the tip of the jaw in larvae shorter than 5.8 mm., but some are present at lengths above 6.8 mm. In larvae over 10.7 mm., melanophores on the lower jaw are found only on the cartilaginous projection (fig. 3A-D).

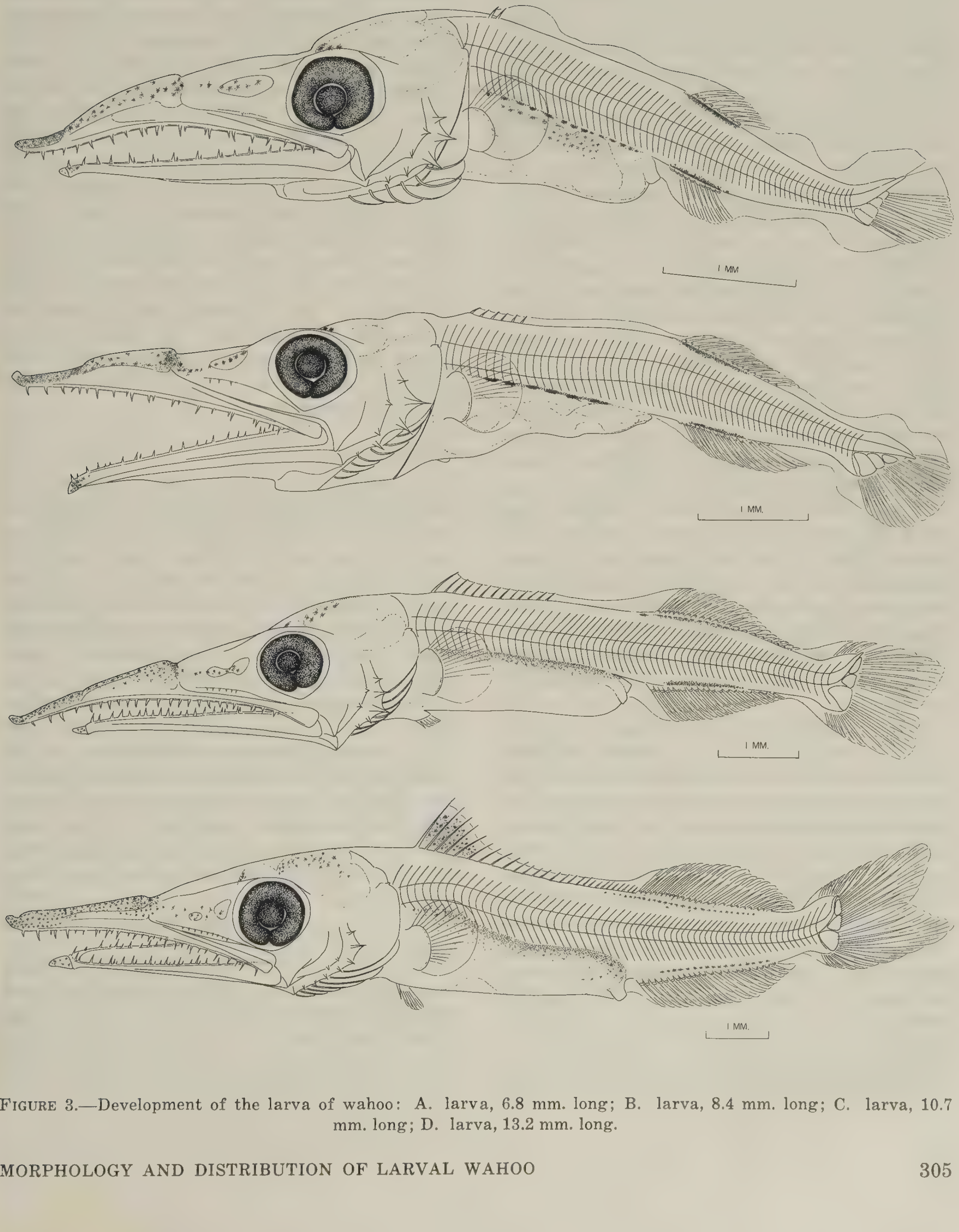
1 MM
1 MM.
1 MM.
1 MM.

FIGURE 3.—Development of the larva of wahoo: A. larva, 6.8 mm. long; B. larva, 8.4 mm. long; C. larva, 10.7 mm. long; D. larva, 13.2 mm. long.

Preanal Trunk Pigmentation

The preanal trunk region is free of dermal pigmentation in larvae smaller than 10.7 mm.; the only pigmentation present is internal, along the dorsal part of the abdominal cavity. The pigmentation here consists of 7 to 10 large pigment spots, each composed of either a single melanophore or several small melanophores which are contiguous. These melanophores can be seen through the thin abdominal musculature in larvae smaller than 8.4 mm. (fig. 2A-D). The number of abdominal melanophores increases and they spread out ventrally over the peritoneum when the larvae are about 6.8 mm. long, but not in all larvae—see, for example, the 8.4-mm. larva of figure 3B. Evidently this spreading of melanophores varies among individuals. The abdominal melanophores of the 10.7-mm. larva have spread ventrally over the dorsal one-third of the digestive tract, and a few dermal melanophores have developed on the surface of the body over the dorsal part of the abdominal region (fig. 3C). Subsequently, only these dermal melanophores are noticeable, owing to a thickening of the abdominal musculature. Dermal pigmentation is lacking along the ventral surface of the body in the abdominal region. The 17.8-mm. larva has about 14 small dermal melanophores on the dorsal part of the first few myomeres, and a wide band of dermal melanophores over the lower half of the body posterior to the pectoral fin. This band extends to the level of the posterior end of the base of the anal fin.

Orton (1953) has shown that in certain teleost larvae, including two scombroids, *Pneumatophorus diego* and *Sarda lineolatus,* the pigment cells along the dorsal region of the body migrate ventrally and that in all pelagic species that she examined the first "wave" of pigment migration is typically completed in 2 days after hatching. In all except one wahoo larvae that I examined, the pigment spots were in a ventral position. One larva had a pigment spot at the nape (fig. 2B); possibly this was a melanophore that had not yet migrated ventrally.

Postanal Trunk Pigmentation

Two stages of pigment formation are evident in the postanal trunk area. The first is seen in larvae less than 4.4 mm. long, which usually have one but sometimes two or three melanophores on the ventral midline of the body near the caudal peduncle, and, in most specimens, a very small melanophore is near and ventral to the posterior end of the notochord (fig. 2A-D). These pigment spots resemble those in larvae of skipjack tuna. The second stage is seen in larvae 5.8 to 6.2 mm. long (fig. 2D); the melanophore at the caudal peduncle region has migrated anteriorly to the base of the anal fin and has increased in size. The 6.8-mm. larva has a group of fine granules of pigment that extend along the base of the anal fin (fig. 3A) in place of the enlarged melanophore; this pattern prevails until the larvae are more than 10.7 mm. long. In the 13.2-mm. larva, the granules of pigment are replaced by a series of evenly spaced melanophores that extend from about the middle of the anal fin to the base of about the eighth anal finlet (fig. 3D).

Fin Pigmentation

Fin pigmentation is not extensive, except on the first dorsal fin. Some fins, the pectoral, pelvic, and caudal, are unpigmented throughout the larval and early juvenile stages. Pigmentation on the first dorsal fin develops when the larvae are 10.7 to 13.2 mm. long. At 13.2 mm., at least the first five interspinous membranes of the first dorsal fin are pigmented with scattered melanophores of various sizes (fig. 3D), and at 17.8 mm., the first eight interspinous membranes are pigmented. In the 17.8-mm. larva, melanophores are also developed on the basal portion of nearly all dorsal and ventral finlets. When the juveniles are about 23.7 mm. long (see Strasburg, 1964: fig. 2), the basal half of the entire first dorsal fin and of all dorsal and ventral finlets is darkly pigmented.

CHANGES IN BODY PARTS

To study the growth of body parts, measurements (table 3) were made as described previously. Measurements of the larger body dimensions, such as standard length, head length, and distance from snout to anus and snout to second dorsal fin, were made to the

TABLE 3.—*Measurements of body parts of larval and juvenile wahoo*

Standard length [1]	Head length	Snout length	Orbit diameter	Premaxillary length [2]	Jaw length		Body depth	Distance snout to:			Pectoral fin length [3]	Pelvic fin length
					Upper	Lower		Anus	First dorsal fin	Second dorsal fin		
Mm.	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
2.8	0.8	0.24	0.26	0.05	--------	--------	0.20	1.8	--------	--------	(0.29)	--------
2.8	.8	.25	.26	.05	0.45	0.45	.20	1.8	--------	--------	(.31)	--------
3.1	.9	--------	--------	--------	--------	.49	.20	1.9	--------	--------	(.29)	--------
3.4	1.0	.33	.33	.05	.53	.53	.20	2.0	--------	--------	(.33)	--------
3.8	1.2	.47	.37	.08	.61	.61	.20	2.4	--------	--------	(.41)	--------
3.9	1.2	.49	.37	.10	.66	.66	.23	2.5	--------	--------	(.41)	--------
4.1	1.2	.49	.39	.10	.69	.69	.24	2.5	--------	--------	(.45)	--------
4.2	1.3	.52	.39	.15	.76	.76	--------	2.5	--------	--------	(.37)	--------
4.3	1.4	.53	.41	.17	.84	.84	.27	2.7	--------	--------	(.41)	--------
4.3	1.6	.74	.41	.27	.94	.94	.29	3.0	--------	--------	(.41)	--------
4.3	1.7	.78	.42	.27	.98	.98	.27	2.9	--------	--------	(.41)	--------
4.4	1.8	.87	.43	.33	1.09	1.03	.27	3.1	--------	--------	(.41)	--------
4.5	1.9	.90	.44	.38	1.15	1.07	.33	3.1	--------	--------	(.47)	--------
4.6	1.9	1.00	.47	.36	1.25	1.16	.38	3.1	--------	--------	(.49)	--------
4.8	2.1	1.10	.49	.49	1.41	1.28	.38	3.3	--------	--------	(.53)	--------
5.2	2.2	1.09	.51	.53	1.39	1.31	.43	3.4	--------	--------	(.49)	--------
5.2	2.3	1.25	.51	.68	1.52	1.39	.44	3.6	--------	--------	(.49)	--------
5.5	2.4	1.25	.54	.61	1.58	1.47	.41	3.8	--------	--------	(.49)	--------
5.7	2.6	1.31	.57	.74	1.63	1.50	.47	3.9	--------	--------	(.61)	--------
5.8	2.4	1.33	.57	.78	1.64	--------	.46	4.1	--------	--------	(.53)	--------
5.8	2.9	1.55	.57	.80	1.83	1.63	.49	4.3	--------	--------	(.59)	--------
5.9	2.7	1.52	.57	.86	1.84	1.64	.49	4.1	--------	--------	(.57)	--------
6.2	2.7	1.64	.57	.94	1.91	1.66	.49	4.3	3.4	4.3	(.53)	--------
6.6	3.3	1.93	.68	1.15	2.30	1.97	.55	4.9	3.5	4.8	.41	--------
6.8	3.3	1.89	.68	1.15	2.35	2.00	.56	4.9	3.7	5.1	.41	Bud
7.4	3.4	1.97	.74	1.23	2.30	1.95	.60	5.2	3.6	5.3	.44	Bud
7.6	3.4	2.01	.78	1.23	2.42	2.11	.64	5.3	3.8	5.4	.61	--------
7.8	3.6	2.13	.78	1.31	2.62	2.17	.64	5.5	3.9	5.5	.66	--------
8.4	3.8	2.46	.82	1.56	2.87	2.34	.70	6.0	4.2	6.3	.73	Bud
8.7	3.9	2.34	.82	1.56	2.85	2.30	.68	6.4	4.4	6.5	.78	Bud
9.0	4.0	2.38	.84	1.60	2.87	2.30	.70	6.4	4.4	6.5	.82	Bud
9.2	4.3	2.54	.90	1.68	3.07	2.46	.94	6.4	4.6	6.6	.82	0.16
10.2	4.9	3.03	1.03	1.97	3.65	2.95	1.07	7.6	5.4	7.8	.86	.10
10.7	4.9	3.07	1.09	2.01	3.77	3.07	1.12	7.7	5.5	8.1	.86	.29
13.2	6.4	3.57	1.40	2.25	4.43	3.69	1.48	9.9	6.7	10.0	1.35	.82
17.8	7.4	4.06	1.72	2.46	5.12	4.18	2.05	12.9	8.0	13.3	1.50	1.44
23.7	9.8	4.61	2.40	2.64	5.66	5.31	2.87	16.0	8.8	16.2	2.00	1.83

[1] Two badly damaged larvae (estimated lengths, 6.6 and 7.9 mm.) were not included in the series.
[2] The distance from tip to anterior edge of mesethmoid, measured along the dorsal profile of the snout.
[3] Length of larval pectoral fin in parentheses.

nearest 0.1 mm. at low magnification (7X objective lens) of a dissecting microscope, but that of the smaller dimensions, such as snout length, orbit diameter, premaxillary length, body depth, etc., were made to the nearest 0.01 mm. at high magnification (30X objective lens). At the higher magnification each division on the disc micrometer represented 0.02 mm.

Plots of body part length against standard length indicated varying degrees of nonlinear growth in premaxillary length, snout length, head length, and in body depth. Because snout and head length were found to be affected greatly by a rapid growth of the premaxillary, snout-less-premaxillary length and head-less-snout length were plotted (fig. 4) and compared against standard length.

The relation of these body parts to standard length is best described by the allometric growth equation,

$$Y = bX\alpha$$

where Y is the body part, X is the standard length, α is the ratio of the instantaneous growth rates of Y and X, and b, is a constant of proportionality, sometimes referred to as the "initial growth constant" (Simpson, Roe, and Lewontin, 1960). This equation when transformed to logarithms

$$\text{Log } Y = \text{Log } b + \alpha \text{ Log } X$$

is linear.

Because not all the points for each body part could be fitted by a single curve, they were separated into several groups, and regression lines were fitted to each group separately. The original data are plotted in figure 4, and the constants for the allometric growth equations are given in table 4. The subdivision of the data was made after they had been tested for deviations from simple allometry as suggested by Richards and Kavanaugh (1945). Such subdivision of data seems justified on the basis of the tests and on the premise that in nature relative growth may deviate considerably from simple allometry, often revealing the existence

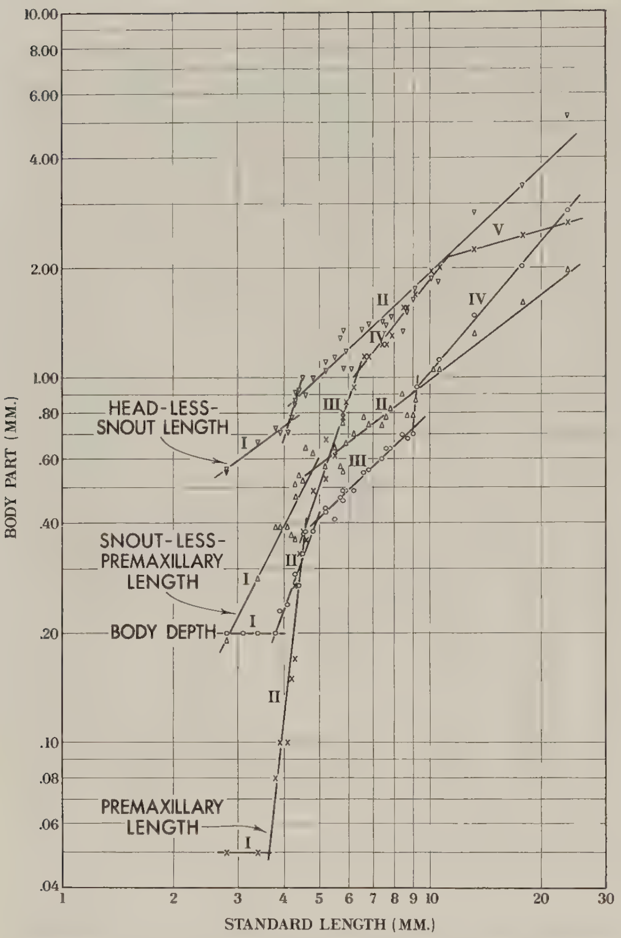

FIGURE 4.—Scatter diagram of body-part measurements plotted against standard length of larval and juvenile wahoo. Straight-line segments are regression lines fitted by the least squares method to respective groups of points. Roman numerals indicate curve segments.

of distinct growth patterns or gradients (Simpson et al., 1960). The subdivision of the wahoo data provides a satisfactory description of the growth relation.

Certain points should be kept in mind when interpreting the curves fitted to the wahoo data. The curves are based on a small number of observations, and some curves are based on a narrow range of standard lengths. Since there is little variability in the wahoo data, the small number of observations appear adequate. The narrow range in standard lengths for some curves appears to be a phenomenon of the growth of many fishes. In addition, it is known that shrinkage of fish larvae occurs in preserved specimens. It is known also that maximum shrinkage occurs within the first few months of preservation and that shrinkage is small after 1 or 2 years, provided there is no drastic change in the amount and concentration of the preservative. As all wahoo specimens had been preserved more than 4 years and were treated in the same manner, the effects of shrinkage are thought to be negligible.

TABLE 4.—*Constants for the allometric equation $Y=bX^{a}$ for larvae and juvenile wahoo collected in the central Pacific Ocean, 1950–62*

Body part	Curve segment	b	a
Premaxillary length	I	0.050	0.000
	II	$.307\times10^{-6}$	9.250
	III	$.445\times10^{-2}$	2.944
	IV	.099	1.273
	V	1.104	.276
Snout-less-premaxillary length	I	.026	1.969
	II	.167	.771
Head-less-snout length	I	.266	.727
	II	$.528\times10^{-2}$	3.500
	III	.216	.951
Depth	I	.200	.000
	II	$.428\times10^{-2}$	2.865
	III	.085	.976
	IV	.069	1.180

A difficulty in dealing with changes in body form in wahoo larvae is that the snout grows much more rapidly than do other parts of the body; this differential growth influences comparisons based on standard length. To determine how snout length influences standard length, I computed regressions of body parts on standard length and on standard length-less-snout length for the four body parts shown in figure 4. Both regression lines showed allometric growth in all four body parts. Since the regressions based on standard length fit the data better than do those based on standard length-less-snout length, standard length was used as the basis of comparison.

Head and Its Components

The most striking change in body form occurs in larvae longer than 3.8 mm., in which head length increases very rapidly. In larvae of this size, head length is nearly one-third of the standard length, but, in larvae 6.6 mm. long, it represents one half the standard length. This large increase in head length is due mostly to rapid growth of the premaxillary.

Five separate curves are required to describe premaxillary growth in wahoo 2.8 to 23.7 mm. long (fig. 4 and table 4). The first curve (larvae 2.8 to 3.4 mm. long) shows no increase in premaxillary length ($\alpha = 0.000$), but the second (larvae 3.8 to 4.4 mm. long) and third curves (larvae 4.5 to 6.2 mm. long) indicate positive allometry ($\alpha = 9.250$ and 2.944, respectively), i.e., the premaxillary grows at a higher rate than standard length or α is greater than 1.0. The fourth curve (larvae 6.6 to 10.7 mm. long) shows only slight positive allometry ($\alpha = 1.273$) and the fifth curve (larvae 13.2 to 23.7 mm. long) represents negative allometry ($\alpha = 0.276$), i.e., the premaxillary grows at a lower rate than standard length or α is less than 1.0.

Growth of the snout less premaxillary can be described by two curves. The first curve (larvae 2.8 to 4.5 mm. long) shows positive allometry ($\alpha = 1.969$), but the second curve (larvae 4.6 to 23.7 mm. long) shows negative allometry ($\alpha = 0.771$).

Because the very rapid growth of the snout (premaxillary included) would mask the growth of the remainder of the head and unduly influence head-length measurements, the head-less-snout length was examined. Regression lines for head-less-snout length are markedly different from those for snout-less-premaxillary and for premaxillary length (fig. 4). In larvae smaller than 4.1 mm., the head-less-snout length increases relatively slower than standard length ($\alpha = 0.727$), but, in larvae between 4.2 and 4.4 mm. long, it increases much faster ($\alpha = 3.500$). Above 4.5 mm. the growth rates of head less snout and standard length are nearly alike ($\alpha = 0.951$).

The sharp increase in the premaxillary and snout affects the appearance of the jaws considerably. In larvae shorter than 4.3 mm., the lengths of the upper and lower jaws are equal (table 5); this condition is typical of larvae of yellowfin tuna, skipjack tuna, and frigate mackerel. At a length of 4.4 mm., however, the upper jaw becomes longer than the lower and remains longer throughout the rest of the larval stages (the difference in length is still apparent in the 23.7-mm. juvenile). The greatest difference in jaw lengths is in larvae between 9.0 and 9.2 mm. long, whose ratios of upper to lower jaw are 1.25:1. This inequality diminishes progressively in larger individuals; in the 23.7-mm. juvenile, the upper jaw is only slightly longer than the lower (ratio, 1.07:1). In the adults the lower jaw is slightly longer than the upper.

TABLE 5.—*Ratios of upper jaw length to lower jaw length, upper jaw length to head length, and lower jaw length to head length by standard length for larval wahoo collected in the central Pacific Ocean, 1950–62*

Standard length	Upper jaw length/lower jaw length	Upper jaw length/head length	Lower jaw length/head length	Standard length	Upper jaw length/lower jaw length	Upper jaw length/head length	Lower jaw length/head length
Mm.				*Mm.*			
2.8	1.00	0.562	0.562	5.8	1.08	0.683	------
3.1	------	------	.545	5.8	1.12	.631	0.562
3.4	1.00	.530	.530	5.9	1.12	.681	.607
3.8	1.00	.508	.508	6.2	1.15	.707	.615
3.9	1.00	.550	.550	6.6	1.17	.697	.597
4.1	1.00	.575	.575	6.8	1.17	.712	.606
4.2	1.00	.585	.585	7.4	1.18	.676	.574
4.3	1.00	.600	.600	7.6	1.15	.712	.620
4.3	1.00	.588	.588	7.8	1.21	.728	.603
4.3	1.00	.576	.576	8.4	1.23	.755	.616
4.4	1.06	.606	.572	8.7	1.24	.731	.590
4.5	1.07	.605	.563	9.0	1.25	.718	.575
4.6	1.08	.658	.610	9.2	1.25	.714	.572
4.8	1.10	.671	.610	10.2	1.24	.745	.602
5.2	1.06	.632	.595	10.7	1.23	.769	.626
5.2	1.09	.661	.604	13.2	1.20	.692	.576
5.5	1.07	.658	.612	17.8	1.22	.692	.565
5.7	1.08	.627	.577	23.7	1.07	.578	.542

The length of each jaw relative to head length also changes significantly. In larvae smaller than 4.3 mm., the ratios of upper and lower jaws to head length are between 0.508:1 and 0.600:1 (table 5). In larvae larger than 4.4 mm., however, the length of the upper jaw increases sharply to a maximum ratio of 0.769:1 in the 10.7-mm. larva, and the lower jaw attains a maximum ratio of 0.626:1. In larvae above 10.7 mm., the ratio of jaw to head length decreases for each jaw; at a length of 23.7 mm. the ratios of the upper and lower jaws to head length are only 0.578:1 and 0.542:1, respectively.

Jaw development is also unequal in larval and juvenile *Scomberomorus* (Hildebrand and Cable, 1938; Eckles, 1949). As in larval wahoo, the longer upper jaw of *Scomberomorus* can be attributed to increased growth of the premaxillary. The premaxillary and head lengths of the wahoo were compared with the same measurements of sierra mackerel (*S. sierra*) and skipjack tuna from the eastern Pacific Ocean (Carlsberg Foundation's "Dana" Expedition 1928-30 and Inter-American Tropical Tuna Commission) and central Pacific Ocean (Bureau of Commercial Fisheries Biological Laboratory, Honolulu) (table 6).

All available data are included in table 7, although the comparison is restricted to individuals between 7.0 and 17.0 mm. because the full range of sizes for the three species was not identical. The ranges of ratios of premaxillary length to head length and the ratios of premaxillary length to standard length are distinctive for each species, and without overlap among the three. The ratio of premaxillary length to head length is largest in wahoo and smallest in skipjack. The lower and upper limits of the range for sierra mackerel (0.221:1-1.250:1) are about 1.71 and 1.54 times greater, respectively, than those for skipjack (0.129:1-0.163:1), and the lower and upper limits of the range for wahoo (0.332:1-0.413:1) are 2.57 and 2.53 times greater, respectively, than those for skipjack. Logarithmic plots of the premaxillary length against standard length (fig. 5) show this more clearly.

TABLE 6.—*Measurements of standard length, head length, and premaxillary length, and ratios of premaxillary length to standard length and premaxillary length to head length of larval and juvenile wahoo, sierra mackerel, and skipjack tuna*

Size	Specimens	Average measurements			Premaxillary length/standard length	Premaxillary length/head length
		Standard length	Head length	Premaxillary length		
Mm.	*Number*	*Mm.*	*Mm.*	*Mm.*		
Wahoo						
2.0-2.9	2	2.8	0.8	0.05	0.018	0.062
3.0-3.9	3	3.7	1.1	.08	.022	.073
4.0-4.9	9	4.4	1.7	.28	.064	.165
5.0-5.9	7	5.6	2.5	.71	.127	.284
6.0-6.9	3	6.5	3.1	1.08	.166	.348
7.0-7.9	3	7.6	3.5	1.26	.166	.360
8.0-8.9	2	8.6	3.8	1.57	.183	.413
9.0-9.9	2	9.1	4.2	1.68	.185	.400
10.0-10.9	2	10.4	4.9	1.99	.191	.406
13.0-13.9	1	13.2	6.4	2.25	.170	.352
17.0-17.9	1	17.8	7.4	2.46	.138	.332
23.0-23.9	1	23.7	9.8	2.64	.111	.270
Sierra mackerel						
7.0-7.9	2	7.4	3.2	.75	.101	.234
11.0-11.9	2	11.6	5.0	1.25	.108	.250
12.0-12.9	3	12.6	5.4	1.33	.106	.248
13.0-13.9	1	13.1	5.9	1.33	.097	.227
14.0-14.9	1	14.0	6.4	1.58	.113	.247
15.0-15.9	2	15.1	6.6	1.54	.102	.234
16.0-16.9	1	16.2	6.8	1.50	.093	.221
17.0-17.9	1	17.3	7.0	1.75	.101	.250
18.0-18.9	2	18.7	7.2	1.62	.087	.225
Skipjack tuna						
5.0-5.9	3	5.6	2.3	.30	.054	.130
6.0-6.9	4	6.7	2.8	.46	.069	.164
7.0-7.9	1	7.8	3.6	.50	.064	.139
8.0-8.9	2	8.5	3.8	.62	.073	.163
10.0-10.9	1	10.2	4.6	.67	.066	.146
11.0-11.9	1	11.8	5.6	.83	.070	.148
12.0-12.9	2	12.6	5.4	.83	.067	.154
13.0-13.9	4	13.4	5.5	.77	.057	.140
14.0-14.9	4	14.2	5.7	.77	.054	.135
15.0-15.9	3	15.4	5.8	.75	.049	.129
16.0-16.9	2	16.4	6.8	.96	.058	.141
17.0-17.9	1	17.6	6.4	.91	.052	.142
18.0-18.9	1	18.1	6.4	.91	.050	.142
23.0-23.9	2	23.9	8.3	.96	.040	.116

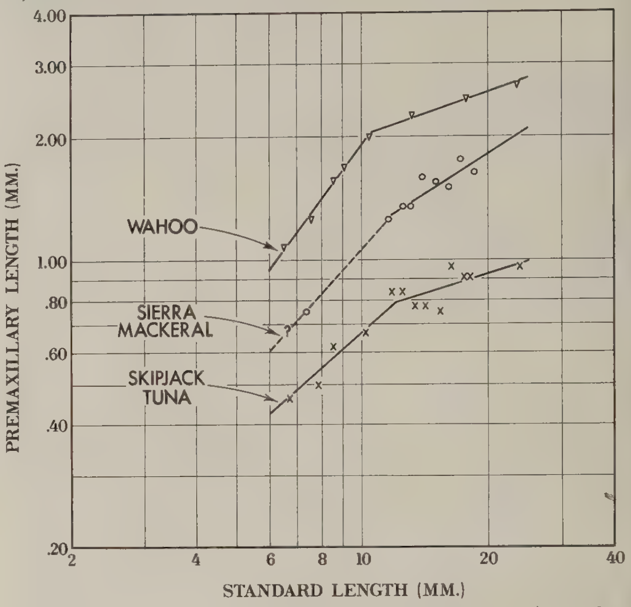

FIGURE 5.—Scatter diagram of premaxillary lengths plotted against standard length of larval and juvenile wahoo, sierra mackerel, and skipjack tuna. Line segments are regression lines fitted by the least-squares method.

These large differences in the ratios of premaxillary length to head length suggest that the size of the premaxillary may be of generic significance. This view is contrary to Conrad's (1938) opinion that the long, pointed premaxillary, thought to be so characteristic of the genus *Acanthocybium*, "is an unfortunate illusion." Conrad based his opinion upon the closeness of the ratios of premaxillary length to skull length of *Scomber* and *Acanthocybium*, 0.23:1 and 0.24:1, respectively; however, a careful check of his ratio for *Scomber* indicates a possible error.

Conrad defined premaxillary length as "the length of premaxillae anterior to the dermethmoid" and length of skull as the length "from anterior tip of premaxillae to posterior tip of supra-occipital crest." He did not give the species name or the source of his *Scomber* measurements, but judging from his numerous citations of Allis (1903) concerning this genus, it is very likely that the measurements were obtained from the figure of *S. scomber* by Allis. Using the reference points defined by Conrad,

TABLE 7.—*Meristic counts of larvae and juvenile wahoo* [1]

Standard length	Myomeres			Branchiostegal rays	Teeth [2]				Fin spines and rays					Caudal fin rays	
	Pre-anal	Post-anal	Total		Upper jaw	Lower jaw	Palatine	Vomerine	First dorsal	Second dorsal plus finlets	Anal plus finlets	Pectoral	Pelvic	Dorsal (principal and secondary)	Ventral (principal and secondary)
Mm.	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
2.8	26	39	65	0	0	0	0	0	0	0	0	0	0	0	0
2.8	29	35	64	0	0	0	0	0	0	0	0	0	0	0	0
3.1	28	37	65	0	0	0	0	0	0	0	0	0	0	0	0
3.4	28	37	65	0	0	0	0	0	0	0	0	0	0	0	0
3.8	30	35	65	0	0	0	0	0	0	0	0	0	0	0	0
3.9	27	37	64	0	0	0	0	0	0	0	0	0	0	0	0
4.1	27	37	64	0	1	0	0	0	0	0	0	0	0	0	0
4.2	29	35	64	0	2	1	0	0	0	0	0	0	0	0	0
4.3	29	36	65	0	3	4	0	0	0	0	0	0	0	0	0
4.3	29	35	64	0	D	D	0	0	0	0	0	0	0	0	0
4.3	30	35	65	0	8	9	0	0	0	0	0	0	0	0	0
4.4	29	35	64	0	7	7	0	0	0	0	0	0	0	0	0
4.5	27	37	64	0	7	8	0	0	0	0	0	0	0	0	0
4.6	27	38	65	0	9	7	1	0	0	0	0	0	0	0	0
4.8	27	37	64	0	10	10	2	0	0	0	0	0	0	0	0
5.2	27	37	64	0	13	13	2	0	0	0	0	0	0	0	0
5.2	27	38	65	1	16	14	2	0	0	0	0	0	0	0	0
5.5	26	38	64	2	15	12	2	0	0	0	0	0	0	0	0
5.7	27	38	65	4	14	14	2	0	0	0	0	0	0	0	0
5.8	28	36	64	3	16	14	2	0	0	0	0	0	0	3+0	3+0
5.8	30	35	65	5	17	15	2	0	0	0	0	0	0	3+0	2+0
5.9	27	36	63	4	17	16	2	0	0	0	0	0	0	3+0	2+0
6.2	26	39	65	5	17	15	3	0	0	0	0	0	0	4+0	3+0
6.6	32	32	64	6	18	16	3	0	0	3	4	4	0	5+0	4+0
6.6 (est.)	27	36	63	5	D	D	D	D	0	5	4	5	0	5+0	4+0
6.8	31	34	65	6	23	20	1	0	2	7	7	4	Bud	7+0	4+0
7.4	26	38	64	6	20	17	3	0	3	9	8	5	Bud	7+0	5+0
7.6	27	37	64	7	21	18	3	0	4	11	10	6	0	7+0	6+0
7.8	29	35	64	6	20	18	3	1?	5	12	11	6	0	6+0	5+0
7.9 (est.)	26	38	64	6	20	20	3	0	5	12	11	7	0	7+0	5+0
8.4	28	37	65	7	22	21	3	1	6	15	14	10	Bud	9+2	8+0
8.7	26	37	64	7	24	20	3	1	6	16	16	11	Bud	9+4	8+2
9.0	26	39	65	7	23	21	3	1	8	20	18	11	Bud	9+3	8+1
9.2	30	35	65	7	24	20	4	1	8	20	19	11	Bud	9+4	8+3
10.2	27	37	64	7	23	20	5	1	10	21	20	12	I, 2	9+4	8+3
10.7	28	36	64	7	23	21	6	2	13	21	20	11	I, 4	9+4	8+3
13.2	29	36	65	7	30	25	9	2	27	23	22	14	I, 5	9+7	8+6
17.8	26	38	64	7	28	24	8	2	27	23	22	19	I, 5	9+9	8+9
23.7	--------	--------	--------	7	28	25	7	2	27	24	22	23	I, 5	9+15	8+15

[1] Standard length (mm.) and numbers of precaudal vertebrae and caudal vertebrae for each of three specimens in which vertebrae were counted were as follows: 13.2 mm.—33, 31; 17.8 mm.—32, 31; 23.7 mm.—32, 31.

[2] D = damaged.

I obtained a premaxillary length to skull length ratio of 0.11:1 for the *S. scomber* illustrated by Allis (1903), and ratios of 0.12:1, 0.12:1, 0.11:1, and 0.10:1 for four *S. japonicus* that were 220, 271, 284, and 386 mm. fork length, respectively. These ratios vary considerably from the 0.23:1 which Conrad reported for *Scomber*.

Strasburg (1964) has mentioned the presence of a small, cartilaginous pad at the tip of the lower jaw in juvenile wahoo. The pad is barely noticeable in the 4.2-mm. larva but is clearly developed in the 4.3-mm. larva. The pad assumes its characteristic conical shape in larvae more than 5.8 mm. long.

Body Depth

In many fish larvae, body depth at the pectoral fin is greatly influenced by the amount of food in the digestive tract. Furthermore, the distention of the gill cover and the bending of the body at the junction of the head and trunk also distort the body depth of fish larvae at the pectoral fin. The variability produced by this distortion can be eliminated by discarding all distorted specimens, but this measure was not possible because few wahoo larvae were available. Consequently, body depth of wahoo larvae was measured at the posterior edge of the anus, where distortions caused by bending are minimal.

Body depth follows a different course of growth from that of premaxillary length. Differences between the two growth curves are seen mainly in larger larvae (fig. 4 and table 4); where the premaxillary grows at a uniform rate in larvae 6.6 to 10.7 mm. long, the body depth increases abruptly when the larvae are about 9 mm. long, and where the premaxillary grows relatively slower than standard length in larvae larger than 10 mm. ($\alpha = 0.276$), the depth increases slightly faster ($\alpha = 1.180$) than the body.

Distance from Snout to Anus

Snout-to-anus distance shows positive allometry, but this phenomenon results from the sharp increase in snout length relative to standard length. If the snout length is subtracted from both snout-to-anus distance and standard length, a linear relation, $Y = -0.09 + 0.623X$, is evident (fig. 6). Thus the snout-to-anus distance, less snout length, increases 0.623 mm. for each 1.0-mm. increase in standard length, less snout length. A linear relation between snout-to-anus distance and standard length also exists in the Pacific mackerel, *Pneumatophorus diego* (Kramer, 1960).

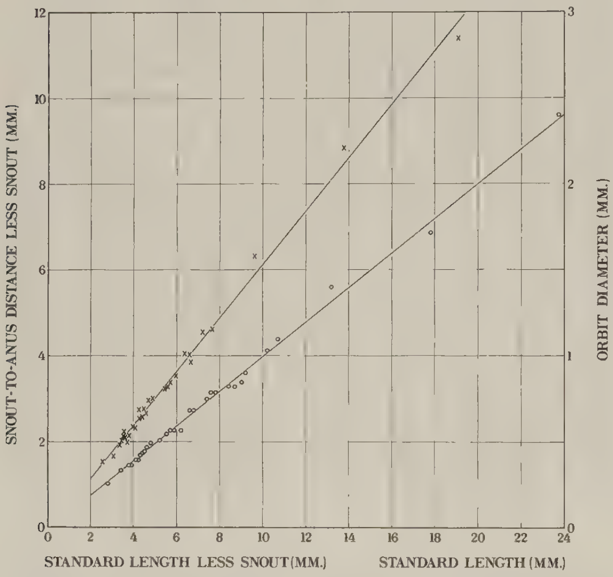

FIGURE 6.—Regressions of snout-to-anus distance less snout on standard length less snout (upper line), and orbit diameter on standard length (lower line). Lines fitted by the method of least squares.

The low rate of increase in the snout-to-anus distance of wahoo larvae is probably related to the shape of the digestive tract and the position of the anus. The digestive tract in wahoo larvae, unlike that in larvae of yellowfin tuna and skipjack tuna, is elongate, and the anus is situated near the origin of the anal fin, i.e., between the 26th and 29th myomeres, in larvae as small as 2.8 mm. (table 7). The anus maintains this relative position throughout the larval and juvenile stages. In yellowfin tuna and skipjack tuna less than 7.0 mm. long, however, the digestive tract is compact and the anus is located at a point midway between the posterior edge of the head and the origin of the anal fin, i.e., between the 9th and 11th myomeres; furthermore, the anus shifts posteriorly as the larvae increase in size, until it is situated near the origin of the anal fin in larvae 11.0 to 13.0 mm. long.

In one respect the digestive tract resembles that of larvae of yellowfin tuna and skipjack tuna: it forms a complete loop, which is clearly visible in larvae 2.8 to 5.8 mm. long (fig. 2A-D). The loop is difficult to see in larvae larger than 6.8 mm. because of the heavier abdominal musculature and the increased pigmentation over the digestive tract (fig. 3A-D). The 4.0-mm. and 5.0-mm. Pacific mackerel larvae illustrated by Kramer (1960) have a similar loop in the digestive tract.

Orbit Diameter

Throughout the size range examined, the relation of orbit diameter to standard length is linear, $Y = -0.019 + 0.0101X$, the orbit increasing 0.101 mm. in diameter for 1.0-mm. increase in standard length (fig. 6). The eye is cleft ventrally.

OSSIFICATION OF SKELETON

Myomeres, vertebrae, teeth, branchiostegal rays, fin rays, and spines were counted (table 7), and the ossification of bones was studied after the larvae had been stained with alizarin. A bone is considered as ossified if it absorbs the stain. Ossification proceeds more slowly in wahoo than it does in some other scombrids. The sequence of ossification is summarized in table 8.

Pectoral Girdle

The cleithrum is one of the first bones to ossify. The process begins in larvae about 2.8 mm. or smaller and is complete at 3.1 mm. or larger.

Upper and Lower Jaws

In the upper jaw, the development of the maxillary and premaxillary is similar to that described for *Trachurus* (Berry, 1964). The

TABLE 8.—*Sequence of ossification of bones of wahoo larvae*

Body part	Fish length at start	Fish length at finish
	Mm.	*Mm.*
Cleithrum	2.8	3.1
Parasphenoid	2.8	3.1
Maxillary	3.1	3.1
Dentary	3.1	3.8
Gill arch	3.4	6.8
Premaxillary	3.8	4.5
Teeth—upper jaw	4.1	----------
Preopercular spines	4.1	----------
Teeth—lower jaw	4.2	----------
Preopercle	4.3	----------
Articular	4.3	4.5
Palatine	4.3	8.4
Vomer	4.5	8.4
Palatine teeth	4.6	13.2
Branchiostegal rays	5.2	8.4
Parietal	5.7	10.7
Frontal	5.7	17.8
Caudal fin (principal rays)	5.8	8.4
Pectoral fin	6.6	23.7
Second dorsal fin and finlets	6.6	10.2
Anal fin and finlets	6.6	13.2
Vertebrae	6.8	17.8
First dorsal fin	6.8	13.2
Vomerine teeth	8.4	----------
Caudal fin (secondary rays)	8.4	<23.7
Pelvic fin	10.2	13.2
Opercle	<13.2	----------
Supraoccipital crest	13.2	>23.7

maxillary ossifies first in larvae about 3.1 mm. long. The premaxillary begins to ossify at about 3.8 mm., but the development is restricted to the anterior half of the jaw. Ossification proceeds posteriad until the full length is developed in larvae about 4.5 mm. long. The premaxillary essentially excludes the maxillary from the gape (i.e., from the functional biting surface of the jaw) by its position ventral to the maxillary.

The lower jaw also has two bones, the dentary and articular. The dentary first develops in larvae about 3.1 mm. long and is completely ossified in larvae over 3.8 mm. Ossification of the articular begins in larvae about 4.2 mm. long and is complete at about 4.5 mm.

Gill Arches

The gill arches do not absorb stain until the larvae are about 3.4 mm. long. After the first arch has ossified, however, subsequent arches develop in quick succession and all are completely ossified in larvae about 6.8 mm. long. As in the adults, the larvae and juveniles have no gill rakers.

Teeth

The teeth in both jaws develop at a smaller size in wahoo larvae than in yellowfin tuna larvae, but slightly later than in skipjack tuna larvae. Teeth in the upper jaw are formed only on the premaxillary, when the larvae are about 4.1 mm. long. The first few teeth appear almost simultaneously as small protuberances. In the lower jaw, teeth develop on the dentary when the larvae are about 4.2 mm. long. About seven widely spaced teeth of uniform size are present in each jaw when the larvae are about 4.4 mm. long. In larvae above 5.8 mm., smaller teeth are added near the bases of the larger ones; at 13.2 mm., one or two small teeth are usually present between two adjacent long teeth (fig. 3D). Initially, when the jaws are of equal length, the number of teeth in each is about equal. As the upper jaw protrudes beyond the tip of the lower jaw, three to four additional teeth appear on the protruded section of the upper jaw (figs. 2D and 3A-D). The three or four anteriormost teeth in the upper jaw become slightly recurved; the teeth posterior to these appear straight and more nearly vertical to the longitudinal axis of the jaw. When the juveniles attain a length of 13.2 mm., about half the number of teeth found in the adults are already ossified; however, the conical shape of the teeth of the larvae differs from the compressed and triangular teeth of the adults.

The palatine bone begins to ossify in larvae about 4.3 mm. long, and ossification is complete at about 8.4 mm. The first palatine tooth develops when the larvae are about 4.6 mm. long. The number of teeth increases slowly and reaches a maximum of nine in the 13.2-mm. larva.

The vomer begins to ossify later than the palatine, when the larvae are about 4.5 mm. long, but completes ossification at the same time as the palatine. The first vomerine tooth is developed in larvae about 8.4 mm. long; two are present at about 10.7 mm., and this number remains constant through the 23.7-mm. stage.

Preopercular Spines, Preopercle, and Opercle

Unlike the preopercular spines of skipjack tuna, which appear when the larvae are about 3.7 to 3.9 mm. total length (Matsumoto, 1958), the preopercular spines of the wahoo appear when the larvae are longer than 4.1 mm., SL. At this stage only a single spine is ossified at the angle of the preopercle. Additional spines develop slowly; at 4.3 mm., only two spines are ossified (fig. 2C). The third spine is first seen on the 4.7-mm. larva, and the fourth and fifth spines appear in larvae longer than 6.8 mm. The number of spines remains constant until the larvae attain a length of 13.2 mm., when two spines are added on the horizontal edge. The 23.7-mm. juvenile possesses the greatest number of spines: five on the horizontal and three on the vertical edge of the preopercle. The preopercular spines of the wahoo are relatively shorter than those in larvae of yellowfin or skipjack tuna, and the preopercle has already overgrown most of the spines in the 13.2-mm. juvenile.

As in larvae of yellowfin and skipjack tuna, but to a lesser degree, additional spine development occurs on a ridge on the preopercular surface anterior to the base of the preopercular spines. In larvae between 4.5 and 5.8 mm., a single short spine is present on this ridge, and two spines are developed in larvae between 6.8 and 10.7 mm. In yellowfin tuna, skipjack tuna, and black skipjack (*Euthynnus* spp.), three or more spines are already present in larvae less than 5.5 mm. total length (cf. Matsumoto, 1958, 1959).

The preopercular surface begins to ossify when the larvae are about 4.3 mm., soon after the first preopercular spine has developed. Ossification starts at the base of the preopercular spine and, as more spines are added, increases correspondingly. When the larvae are 7.4 mm. long, a small portion of the dorsal and ventral terminals of the preopercle also becomes ossified. The surface of the preopercle is almost completely ossified in the 23.7-mm. juvenile.

In larvae of yellowfin tuna, skipjack tuna, and black skipjack, between 5.0 and 6.0 mm. total length, a conspicuous spine develops in the posttemporal region of the head. This spine is absent in wahoo; instead it is represented by a bony ridge which is present throughout the larval and juvenile stages. This ridge is first apparent in the 8.4-mm. larva. A second ridge is seen dorsal to the first, and a groove appears between the two ridges in the 23.7-mm. juvenile. I presume that with continued growth of the juvenile, these two ridges unite to form a canal that becomes part of the lateral line system.

The opercle begins to ossify when the larvae are about 13.2 mm. long. Ossification progresses slowly, and the opercle is still not completely developed at 23.7 mm.

Branchiostegal Rays

The first branchiostegal ray is seen in the 5.2-mm. larva. The number of rays increases to four in the 5.7-mm. larva and to six in larvae 6.6 to 6.8 mm. long. The full complement of seven rays is generally ossified in larvae about 8.4 mm. (fig. 3B), although a 7.6-mm. larva already had seven rays. The posteriormost ray ossifies first, and subsequent ossification proceeds anteriorly.

Other Head Bones

The parasphenoid first begins to ossify in larvae 2.8 mm. or smaller, and its entire length is ossified in about 3.1 mm.

It is difficult to determine the initial development of the frontal and parietal bones because these bones did not stain sufficiently in some of the specimens. The first sign of ossification appears in the 5.7-mm. larva. The parietal bone develops faster than the frontal bone and is completely ossified in larvae 10.7 mm. long. The frontal bone, on the other hand, is completely ossified only in the 17.8-mm. larva and the 23.7-mm. juvenile.

In contrast to these three bones, ossification of the supraoccipital crest, which develops only after nearly all the fin rays and vertebrae have completely ossified, starts in larvae about 13.2 mm. long. Ossification is completed only after the individuals exceed 23.7 mm.

Fins

The sequence of fin formation in wahoo larvae is similar to that of jack mackerel and Pacific mackerel (Ahlstrom and Ball, 1954; Kramer, 1960); the only difference is in the length of body at which fin development commences. In all fins, the actinotrichia first develop in the larval fin fold. These are replaced by definitive rays, lepidotrichia, which are branched, jointed rays composed of bone. Fin spines arise by alteration and fusion of the joints of the lepidotrichia. The fins will be discussed in the order of their formation: (1)

larval pectoral (without rays), (2) caudal, (3) pectoral, (4) second dorsal and anal, (5) first dorsal, and (6) pelvic.

Larval pectoral fins.—The larval pectoral fins are formed on the smallest larva, 2.8 mm. long. The fin membrane is large and fanshaped, and fin rays do not develop until the larvae are well past 6 mm. (table 8).

Caudal fin.—The caudal fin of wahoo develops first as a thickening ventral to the posterior portion of the notochord in larvae about 4.4 mm. long (fig. 2C). As the size of this thickening increases, the posterior portion of the notochord turns upward; at this stage the larvae are shorter than 6.8 mm. (fig. 3A). This thickening eventually develops into the hypural bones.

The principal caudal rays, those that are ultimately supported by the hypural bones, develop before any of the secondary caudal rays are formed. When the larvae are about 5.8 mm. long, the first two to four rays near the middle of the posterior edge of the hypural thickening develop almost simultaneously. The midline separating the ultimate dorsal and ventral lobes of the tail is clearly discernible, owing to the wide spacing between the two medial rays. The initial group of rays lies at an oblique angle to the notochord, but as the posterior part of the notochord turns upward, it pulls the rays up to a horizontal position. Subsequent ray development proceeds dorsally and ventrally from the medial rays. As in most percomorph fishes, there are 17 principal caudal rays in the wahoo: 9 are dorsal and 8 ventral to the midline of the fin. All the principal rays are completely developed in larvae over 8.4 mm. long (fig. 3B).

The secondary caudal rays first appear on larvae about 8.4 mm. long with the development of two dorsal rays anterior to the tip of the notochord. The sequence of ossification is from posterior to anterior for both the dorsal and ventral secondary rays. At a length of 23.7 mm., the caudal fin has 15 dorsal and 15 ventral secondary rays, which is within the range for adults.

The shape of the caudal fin changes as the rays are being developed. At first the larval caudal fin, represented by the median fin fold, is roundly lobed. As the principal rays develop, the initial medial rays are longer than the rest of the fin fold. With the flexion of the notochord and the subsequent shift in position of the rays to a horizontal plane, the fin outline becomes angular (fig. 3A). After all the principal rays have developed, the dorsal and ventral rays begin to outgrow the medial rays, so that the posterior margin of the fin gradually assumes a square and finally a forked shape. The fork in the caudal fin is evident in the 10.7-mm. larva (fig. 3C) and is pronounced in larvae above 13.2 mm. long (fig. 3D).

Pectoral fins.—The larval pectorals already are present in the smallest wahoo (fig. 2A). The initial pectoral rays begin to develop near the dorsal part of the fin when the larvae are about 6.6 mm. long, and are much shorter than the pectoral membrane. At a length of 8.4 mm., these rays extend to the margin of the larval pectoral fin. As is usual in pectoral-fin development, the dorsal rays appear first. Twenty-three pectoral rays are developed in the 23.7-mm. juvenile. This total is within the range for adults.

Second dorsal fin and finlets.—The base of the second dorsal fin first appears as a thickening on larvae as small as 5.8 mm., and the first rays are developed in larvae 6.6 mm. long. The first two or three rays develop simultaneously near the middle of the fin; subsequent rays develop anteriorly and posteriorly to these. The first few finlets develop before the formation of the anteriormost ray of the second dorsal fin. The last finlet, however, develops only after the formation of all the second dorsal fin rays.

In the early stages of development, it is extremely difficult to differentiate rays from finlets. Consequently, the number of ray and finlet elements for the larvae were combined. A similar grouping for the adults shows that the full complement of rays and finlets for the second dorsal fin ranges from 20 to 22 (table 2). As discussed earlier, two elements, which are separated in the larvae, form the last adult finlet. Consequently, the total number of larval fin ray and finlet elements comparable with those of the adult must be more than 21. The full complement of rays and finlets in the second dorsal is already present in the 13.2-mm.

larva (table 7). The last two finlets in the 23.7-mm. juvenile (Strasburg, 1964: fig. 2) are situated very close together but are not yet fused.

Anal fin and finlets.—Ossification of anal fin rays occurs simultaneously with that of the second dorsal fin. Although subsequent development of rays and finlets is nearly identical with that of the second dorsal fin and finlets, the adult complement is not attained until the juvenile has exceeded 10.7 mm. long. All the rays and finlets are completely formed in the 13.2-mm. larva. As in the dorsal finlets, the last two anal finlets on the 23.7-mm. juvenile (Strasburg, 1964: fig. 2) are very close together, their bases nearly touching each other.

First dorsal fin.—As in the anal and second dorsal fins, the base of the first dorsal fin thickens when the larvae are about 6.2 mm. long. The first two or three spines develop almost simultaneously and are first seen in the 6.8-mm. larva (fig. 3A). The first spines are short (0.10 mm.), and, unlike the sequence of ray development in the anal and second dorsal fins, subsequent spines are added only posteriorly. Additional spines develop slowly; the number increases from 2 in the 6.8-mm. larva to 10 in the 10.2-mm. larva. In larvae over 10.2 mm. long, however, the spines are added more rapidly, so that 27 spines are already evident in the 13.2-mm. larva (table 7).

The height and shape of the fin also change with growth of the larvae. Larvae between 8.4 and 8.7 mm. long have all six spines of equal height. Shortly thereafter, the anteriormost spine becomes the longest and each succeeding spine is shorter than the one preceding it. A concavity in the fin outline becomes noticeable after the eighth or ninth spine has ossified (i.e., when the larvae are about 9.0 or 10.0 mm. long). All spines after the ninth are about equal in height (fig. 3D).

Pelvic fins.—The pelvic fins are the last to develop. They appear first, as a protuberance on the ventral contour of the body below the pectoral fin base, in larvae between 6.8 and 9.0 mm. Unlike the interradial membranes of other fins, which develop from the larval fin fold, those of the pelvic fins grow out from the fin base. Initially, the spine and one or two rays ossify almost simultaneously and are first noticed in the 9.2-mm. larva. Both spine and rays are short (0.29 mm.), but their length increases rapidly, so that in the 17.8-mm. larva (table 3), the longest pelvic fin ray (1.44 mm.) is almost as long as the longest pectoral ray (1.50 mm.). The full complement of one spine and five rays is completely formed in juveniles longer than 13.2 mm.

Vertebral Column

In the wahoo, as in many other fishes, the vertebral spines ossify before the centra. A vertebra is considered to be developing as soon as any part begins to ossify, as indicated by stain absorption. Because the anterior abdominal vertebrae, which develop first, lack haemal spines, the ossification of the neural spines is the first stage of vertebral development. Neural spines first appear in wahoo at 6.7 mm. The number of neural spines increases rapidly from 1 in the 6.8-mm. larva to 10 in the 8.4-mm. larva. All the neural and haemal spines are partially or completely ossified in the 13.2-mm. larva, and all the centra in the 17.8-mm. juvenile.

The sequence of development of the centra is from anterior to posterior, in the order of their position. As in the Pacific mackerel, ossification of the centrum starts at the dorsal and ventral portions and progresses laterally until the two ossified portions meet at the midline. The dorsal portion of the first six centra and the ventral portion of the first four are ossified in the 8.4-mm. larva. In the 13.2-mm. larva, the first 10 centra are completely ossified, the 11th to 22d centra are partially ossified, and the dorsal and ventral portions of the 23d to 34th centra are beginning to ossify. The ventral portions of the two centra anterior to the last one, which give rise to the urostyle, also begin to ossify in the 13.2-mm. larva. The remaining 26 centra become ossified between lengths of 13.2 and 23.7 mm.

The urostyle first develops in larvae about 8 mm. long and is completely ossified in larvae larger than 13 mm. In the 13.2-mm. larva, only about half the area of the largest hypural element is ossified. The early development of the urostyle and the last two centra is similar to the ossification in Pacific mackerel (Kramer, 1960). All the bones in the hypural complex are completely ossified in the 17.8-mm. larva.

The neural spines are initially based on the anterior end of their centra. As each centrum grows progressively longer, the base of the corresponding neural spine seems to shift posteriorward, until it is near the middle of the centrum. This change in position of the base of the neural spine is evident in the last six vertebrae (excluding the terminal vertebra) of the 23.7-mm. juvenile. In the adult the bases of the 50th to 59th neural spines have shifted further caudad, to the posterior edge of their corresponding centrum.

The haemal spines, which first appear near the anterior part of the centra, generally remain in their original position throughout the larval stage. In the juvenile stage the bases of the last six or seven haemal spines have shifted posteriorward to the middle of the centrum. This condition is evident in the 23.7-mm. juvenile and is similar to that found in the adult, in which the bases of the 53d to 58th haemal spines have shifted further caudad to the posterior edge of their corresponding centra. This posterior shifting of the neural and haemal spines and the simultaneous decrease in the angle formed by the spines and longitudinal axis of the vertebral column produce the narrow caudal peduncle so characteristic of the scombrids.

Unlike the Pacific mackerel, which develops zygapophyses at about 8.7-mm. body length (Kramer, 1960), the wahoo develops zygapophyses when the larvae are 17.8 to 23.7 mm. long. No zygapophysis is ossified in the 17.8-mm. larva, but in the 23.7-mm. juvenile, the neural prezygapophyses of the 2d to 61st vertebrae and the neural postzygapophyses of the 1st to the 60th vertebrae are ossified. Some differences exist between juvenile and adult neural postzygapophyses of vertebrae near the caudal end. Neural postzygapophyses are widely separated from the bases of the neural spines in juveniles, but in adults those of the 54th to 62d vertebrae have become partially or entirely fused to the neural spines, as each succeeding spine gradually inclines toward the horizontal axis of the vertebral column.

The haemal zygapophyses also ossify when the larvae are between 17.8 and 23.7 mm. long. No haemal zygapophysis is developed in the 17.8-mm. larva, but most of the adult complement are ossified in the 23.7-mm. juvenile. In the latter specimen, the first haemal prezygapophysis is seen on the 27th vertebra; the first two or three appear as small projections near the anterior edge of the centrum and anterior to the base of the haemal arch. All succeeding vertebrae possess haemal prezygapophyses. These structures are presumed to develop anteriorly from the 27th vertebra as the juveniles increase in length, since in the adults the anteriormost haemal prezygapophysis is on the 19th to 21st vertebra.

The haemal postzygapophyses follow a sequence of ossification slightly different from that of the prezygapophyses. In the 23.7-mm. juvenile, haemal postzygapophyses are ossified on the 11th to the 60th vertebra. In the adults, haemal postzygapophyses are present on about the 6th to 57th or 58th vertebra. Consequently, I presume that, as the fish matures, ossification of haemal postzygapophyses continues anteriorly, and the postzygapophyses of the last five or six caudal vertebrae fuse with the haemal spines.

Clothier (1950) called the processes of the haemal arches the haemapophyses and named as parapophyses "the bony projections on each side of the anterior ends of the centra in the abdominal region to which the ribs are attached." I shall use these two terms as defined by Clothier. Perhaps some of the parapophyses and haemapophyses are already ossified in the 10.7-mm. larva, but this cannot be determined because the vertebral column of this specimen did not stain adequately. The anteriormost parapophysis on the side of the centrum is developed on the 13th vertebra in the 13.2-mm. larva, and the anteriormost haemapophysis is developed on the 18th. In the 17.8-mm. larva and the 23.7-mm. juvenile, the anteriormost parapophysis is seen clearly on the third vertebra in the dorsal third of the centrum, which is the adult condition. The parapophyses on succeeding vertebrae are situated progressively lower on the side of the centrum, and the first pair of haemapophyses at the ventral surface of the centrum is ossified on the 17th vertebra.

To trace the development of the haemapophyses on larger wahoo, two juveniles, 152- and 159-mm. SL taken from stomachs, and two adults, 1,066- and 1,252-mm. fork length, were examined. Additional information from an adult 1,468 mm. long (type of length measurement not clearly defined) was obtained from Conrad (1938). The vertebra on which the anteriormost haemapophysis is located, listed in the order of fish size (length in millimeters shown in parentheses), is as follows: 17th (23.7), 12th (152), 13th (159), 14th (1,066), 15th (1,252), and 16th (1,468). This sequence suggests first, that after the initial ossification of the anteriormost haemapophysis on the 17th vertebra in the smallest juvenile, other haemapophyses develop anteriorly until the maximum number has been attained at a length of about 152 mm.; second, that as the fish increase in size, the position of the anteriormost haemapophysis apparently moves posteriorly, probably because of a gradual upward shift in the position of the haemapophysis on the centra as the vertebrae increase in size.

The development of the anteriormost haemal arch also suggests a shift in position. The position of the initial haemal arch shifts from the 23d or 24th vertebra in the juveniles to the 26th or 27th vertebra in the adults.

OCCURRENCE AND DISTRIBUTION OF WAHOO

The adult wahoo are generally found in tropical and subtropical waters and are taken as incidental catches by surface trolling and longlining. In both types of fishing, however, the catches are small: in the central Pacific Ocean only 236 wahoo were caught in 8,937 line-hours of trolling (Murphy and Ikehara, 1955) and 58 wahoo were taken on 14 POFI (now BCF Biological Laboratory, Honolulu) longline fishing cruises, during which 94,128 hooks had been fished at 450 fishing stations (Murphy and Shomura, 1953a, 1953b, 1955; Shomura and Murphy, 1955). Results of surface trolling within a few kilometers of land in the Line Islands in 1955 have led Iversen and Yoshida (1957) to infer that wahoo prefer shallow depths and are more abundant close to shore.

To determine whether the wahoo are taken on the longline more commonly in inshore than in offshore areas (areas less than or greater than 110 km. from land), I plotted the locations where wahoo were taken on the longline (fig. 7) and tested the catch data. The catches in the two areas were not statistically significant.

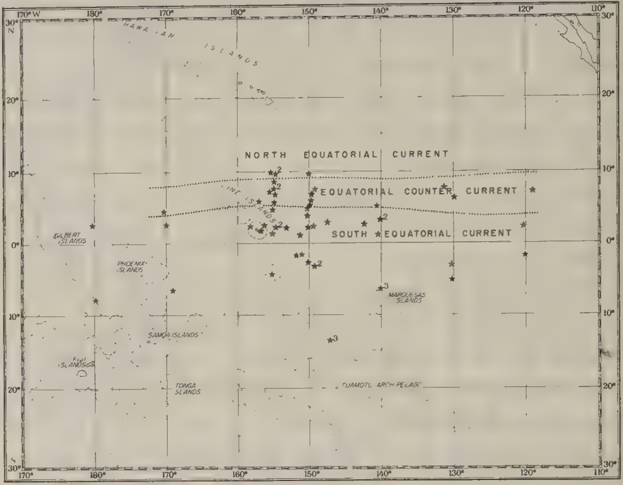

FIGURE 7.—Location and number of adult wahoo taken during 14 POFI (now Biological Laboratory, Honolulu) longline cruises. Each star represents a single wahoo taken at a fishing station. A star and number show catches of two or more wahoo per station. Broken lines around islands indicate a distance of 110 km. from land. Major currents in the central Pacific Ocean are shown.

Larval wahoo were found also in tropical and subtropical waters of the Pacific Ocean between lat. 30° N. and 25° S., and between long. 175° E. and 115° W., the east-west extent of sampling along the Equator. Interestingly, differences between the catches of wahoo larvae in inshore and offshore areas (areas less than or greater than 110 km. from land) were not significant; 12 larvae were caught in 11 of 566 plankton net hauls in inshore areas and 26 larvae were caught in 23 of 1,077 net hauls in offshore areas. The distribution of catches of larvae (fig. 1), moreover, resembled that of the adults taken on the longline.

Of particular interest to this study are (1) the captures of larvae and adults far from land and (2) the scarcity of larvae in the Equatorial Countercurrent (fig. 1), although adults have been taken there on a number of longline stations (fig. 7). One site of larval capture, lat. 8°42′ S. and long. 115°39′ W., was 2,057 km. from the nearest land mass, Ducie Island. This distance is only 181 km. less than the greatest distance from land where an adult wahoo has been taken. Six other capture sites were farther than 900 km. from land. Although adults frequent the Equatorial Countercurrent, they may not spawn there in appreciable numbers. Only one wahoo larva was taken there, representing a catch rate of 0.14 larva per tow.

More adult wahoo are taken around the Hawaiian Islands in summer (April through August) than in other seasons (Welsh, 1949). Seasonal trends are absent, however, near the Equator and around the Line Islands (Iversen and Yoshida, 1957), as they also were in the longline catches made on the 14 POFI cruises (table 9) between lat. 14° N. and 14° S. Most of the fishing on these cruises was done between lat. 9° N. and 8° S.

Monthly catches of larval wahoo show similar trends (table 10). In the area near the Hawaiian Islands (Area I) larvae were taken only in the summer and early fall (May through September), but in the equatorial region (Area II) they were taken in nearly all months of the year.

TABLE 9.—*Adult wahoo caught on 14 POFI longline cruises in the central Pacific Ocean between lat. 14° N. and 14° S.*

Month	Wahoo caught	Catch of wahoo/ 1,000 hooks
	Number	*Number*
January	1	0.29
February	8	.96
March	6	1.33
April	0	.00
May	2	.29
June	4	.72
July	6	2.70
August	14	.69
September	6	.40
October	3	.30
November	4	.37
December	4	.56

TABLE 10.—*Catch rate of wahoo larvae and number of plankton samples collected by months in three areas* [1] *of the central Pacific Ocean, 1950–62*

Month	Area I		Area II		Area III		All areas
	Larvae per 100 samples	Plankton samples	Larvae per 100 samples	Plankton samples	Larvae per 100 samples	Plankton samples	Plankton samples
	Number	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
January	0.0	34	1.8	109	-------	-------	143
February	.0	23	1.0	96	3.4	29	148
March	.0	83	2.1	195	4.2	48	326
April	.0	32	6.1	49	-------	-------	81
May	4.2	96	2.9	34	-------	-------	130
June	4.8	21	1.8	111	-------	-------	132
July	6.1	66	2.4	42	-------	-------	108
August	3.3	180	1.2	81	-------	-------	261
September	3.2	31	0.0	45	-------	-------	76
October	2.6	39	1.3	75	-------	-------	114
November	0.0	53	0.0	46	0.0	2	101
December	-------	-------	8.7	23	-------	-------	23
All months	2.6	658	2.0	906	3.8	79	1,643

[1] Area I from lat. 30° to 15° N.; Area II from lat. 14° N. to 14° S.; Area III from lat. 15° to 25° S.

SUMMARY

Thirty-eight wahoo larvae were taken in a 1-m. plankton net during 32 cruises of the Bureau of Commercial Fisheries research vessels, *Hugh M. Smith* and *Charles H. Gilbert,* in the central Pacific from May 1950 to July 1962. The standard lengths of these specimens ranged from 2.8 to 17.8 mm. In addition, six adults and four juveniles from other sources were examined.

Published accounts of adult wahoo give a vertebral formula, 23 to 33 precaudal +31 to 34 caudal = 54 to 66 total vertebrae, which is an extremely wide range of variation for a fish belonging to the Scombridae. All studies based on examination of specimens indicate only minor variation (31 to 33) in the number of precaudals. Consequently, I conclude that the wide range of precaudal vertebrae first credited to Kishinouye (1923) is incorrect and that the lower figure of 23 precaudals must be a typographical error—a transposition of digits from 32 to 23.

The number of first dorsal spines is constant at 27 in both juveniles and adults. The number of finlets in juveniles is greater than that in adults by one, owing to the fusion of the last two finlets in adults.

Body pigmentation is relatively sparse in larvae smaller than 3.4 mm.; a few melanophores occur on the tip of each jaw, one in each primordial nasal cavity, one on the ventral margin of the caudal peduncle, and a series of about nine evenly spaced along the dorsal surface of the digestive tract. The most noticeable change in pigmentation occurs in larvae above 5.8 mm., when the melanophore at the caudal peduncle migrates to the base of the anal fin and there the number increases until a series of melanophores forms over the entire base of the anal fin. A similar series of melanophores develops at the base of the second dorsal fin. The only other significant increase in pigmentation is in the first dorsal fin just before the larva reaches a length of about 13.0 mm.

Premaxillary length, snout length less premaxillary length, head length less snout, body depth at anus, and snout-to-anus distance less snout show allometric growth that can be described by the equation, $Y = bX_\alpha$.

The most striking change in body form occurs in larvae longer than 3.8 mm., in which head length increases very rapidly. Most of this increase is due to the rapid growth in the premaxillary and snout. The shape and size of the mouth also are affected by the rapid growth in premaxillary and snout. Prior to attainment of 4.3 mm., both jaws have the same length; subsequently, the upper jaw protrudes beyond the lower, and at about 9.0 mm., the ratio of upper to lower jaw is 1.25:1. This ratio decreases to 1.07:1 in the 23.7-mm. juvenile, and in adults the upper jaw is equal to or slightly shorter than the lower. Before unequal jaw development begins, the ratios of upper and lower jaws to head length is between 0.508:1 and 0.601:1. After their lengths become unequal, the ratios of upper and lower jaws to head length increase to 0.769:1 and 0.626:1, respectively.

Body depth increases unevenly throughout the size range. The most rapid growth occurs in larvae between 9.0 and 9.2 mm. long.

Snout-to-anus distance less snout length is linearly related to standard length less snout length. It increases 0.623 mm. for each millimeter increase in standard length less snout length.

Unlike the digestive tract of larvae of yellowfin tuna or skipjack tuna, which is compact (anus located well ahead of the origin of the anal fin), the digestive tract of wahoo larvae is fully extended (anus located close to the origin of the anal fin). The digestive tract of wahoo resembles that of yellowfin tuna and skipjack larvae in that it forms a complete loop.

Orbit diameter is linearly related to standard length. It increases 0.101 mm. for each millimeter increase in standard length.

Ossification of bones and hard parts differs only slightly from the sequence found in jack mackerel and Pacific mackerel. The sequence in wahoo is as follows: Cleithrum and parasphenoid, maxillary and dentary, gill arches, premaxillary, teeth of upper jaw, preopercular spines, teeth of lower jaw, preopercle, articular, palatine, vomer, palatine teeth, branchiostegal rays, parietal, frontal, principal rays of caudal fin, pectoral fin, second dorsal and anal fins simultaneously, vertebrae, first dorsal fin, vomerine teeth, secondary caudal rays, pelvic fins, opercle, and supraoccipital crest.

Wahoo larvae were found in tropical and subtropical waters between lat. 30° N. and 25° S., and between long. 175° E. and 115° W., the east-west extent of sampling along the Equator. The numbers of larvae and adults caught inshore (less than 110 km. from land) and offshore were not significantly different. Wahoo larvae were taken mostly during the summer in the area north of lat. 15° N., and throughout the year along the Equator between lat. 14° N., and 15° S.

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SEASONAL DISTRIBUTION AND RELATIVE ABUNDANCE OF PLANKTONIC-STAGE SHRIMP (*Penaeus spp.*) IN THE NORTHWESTERN GULF OF MEXICO, 1961[1]

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ABSTRACT

Planktonic stages of shrimp (*Penaeus* spp.) were sampled systematically in the Gulf of Mexico near Galveston, Tex., during January-December 1961. The Gulf-V plankton net was used every 3 weeks at stations established at water depths of 14, 27, 46, and 82 m. The study area encompassed about 20,725 km.^{2}

Trends in seasonal abundance of larvae varied with depth. At 14-m. stations a unimodal trend was observed, and peak abundance was during May to September. In deeper waters a bimodal trend was apparent; peak abundance extended from late summer through fall. At all depths, trends in larval abundance increased as bottom water temperatures increased.

Postlarvae were taken in plankton tows during January to April but were most abundant during August to December.

Distinct shifts in the areal distribution of larvae and postlarvae were apparent. During January to March, larvae were restricted to water deeper than 14 m. and shallower than 82 m. whereas postlarvae occurred in all depths. This situation was generally reversed in April to August, when larvae were at all depths, but the distribution of postlarvae was restricted. In September to December, distribution patterns of larvae and postlarvae were generally similar.

On the basis of this study and laboratory experiments on larval development and postlarval growth rates as affected by temperature, support is given to the premise that brown shrimp larvae or postlarvae, or both, overwinter in waters over the Continental Shelf.

The shrimp fishery in the Gulf of Mexico has expanded rapidly within the past 20 years and is now the most valuable fishery in the United States. Since 1950 the yearly harvest has fluctuated around 200 million pounds. Although about six members of the family Penaeidae are taken in the fishery, only three species—the brown shrimp, *Penaeus aztecus* Ives; the pink shrimp, *P. duorarum* Burkenroad; and the white shrimp, *P. setiferus* (Linnaeus)—contribute significantly to the catch.

Before 1959, research designed to provide management programs for optimum utilization of these shrimp stocks did not increase at the same rate as the value of this fishery. In 1959, however, the Bureau of Commercial Fisheries began a program of shrimp research that has expanded considerably during the past 7 years. The general aims of the program were stated by Kutkuhn (1963). The present study of the seasonal distribution and abundance of planktonic-stage *Penaeus* spp. in the northwestern Gulf of Mexico is a part of this research.

Considerable information has been published on the early life history of the white shrimp (Weymouth, Lindner, and Anderson, 1933; Burkenroad, 1934; Pearson, 1939; Anderson, King, and Lindner, 1949). Brown and pink shrimp have similar early life histories, although bathymetric and geographic distributions of the adults are different. In general, these shrimp spawn in waters over the Continental Shelf; brown shrimp spawn at least as far as 198 km. (110 nautical miles) offshore in depths as great as 110 m. The eggs are slightly denser than sea water and settle to the bottom when spawned. After hatching, the young become planktonic and develop through three larval (naupliar, protozoeal, and mysis) and several postlarval stages. They enter the estuaries as postlarvae, grow rapidly to subadult size, and then migrate offshore to complete their growth and spawn.

The earlier work on white shrimp provides

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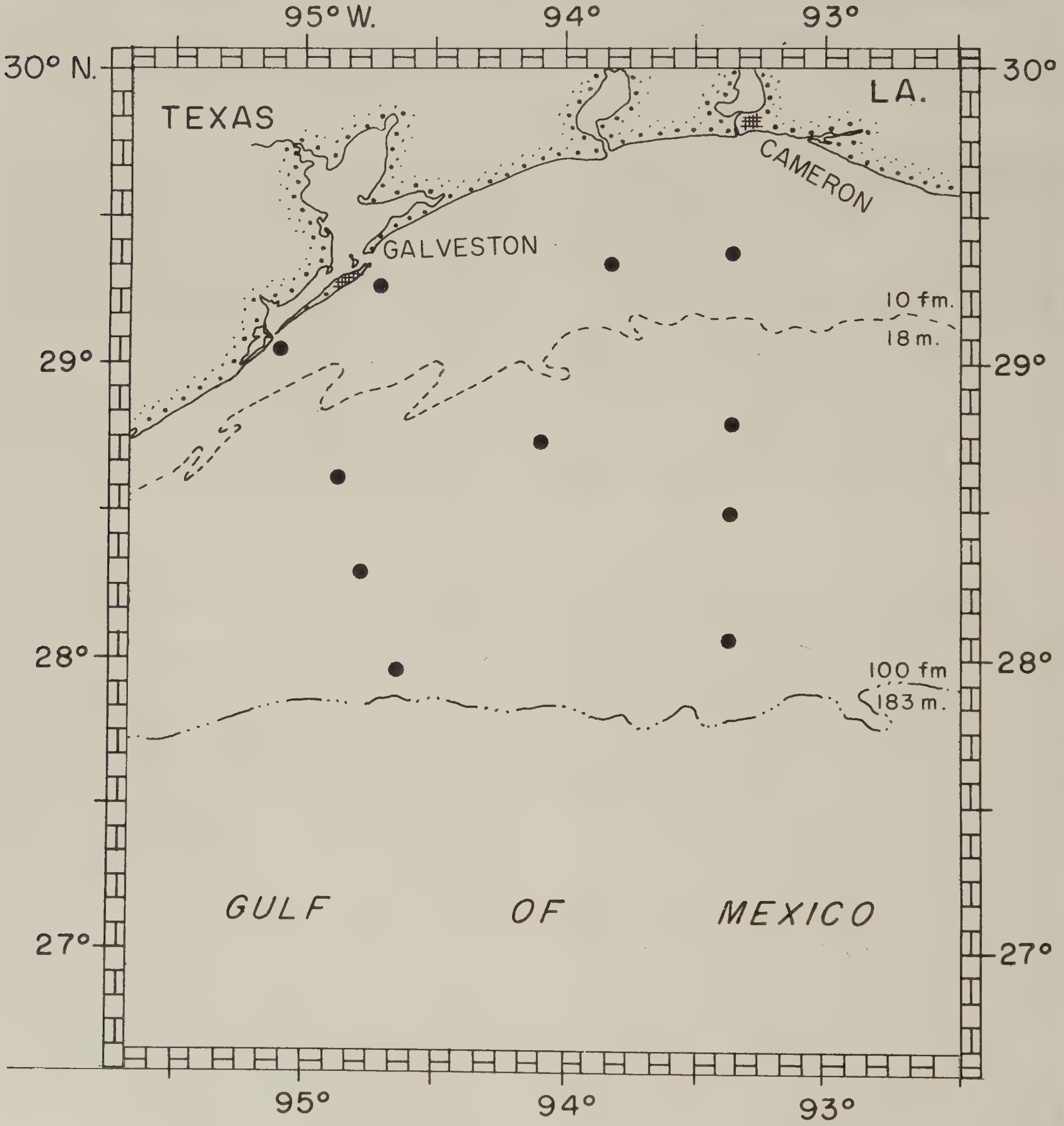
little information about the seasonal distribution, abundance, and taxonomy of planktonic stages of penaeids in the Gulf of Mexico. Until recently the most extensive work available was that of Pearson (1939), who not only described planktonic stages of several penaeids from specimens obtained from plankton hauls, but also provided information on seasonal occurrence and distribution of postlarval white shrimp. More recently, descriptions of plank-


95° W.
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28°
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GULF
OF
MEXICO
27°
27°
95°
94°
93°

FIGURE 1.—Location of sampling stations for shrimp larvae in 1961.

tonic stages have been published for the pink shrimp by Dobkin (1961); for the seabob, *Xiphopeneus kroyeri* (Heller) by Renfro and Cook (1963); and for the rock shrimp, *Sicyonia brevirostris* Stimpson by Cook and Murphy (1965). All three species occur in the northern Gulf.

Because of the limited amount of taxonomic material available, as well as the occurrence of about 35 penaeids (Burkenroad, 1936; Springer and Bullis, 1956; Bullis and Thompson, 1965) in the Gulf of Mexico, one of the major problems in this study was the identification of the planktonic stages. Although H. L. Cook (personal communication) has been able to rear the planktonic stages of brown, white, and pink shrimp, differentiation of the species among these forms is not yet possible. Consequently, penaeids encountered in plankton samples were identified only to genus by using the generic key developed by Cook (1966a). Data on only *Penaeus* spp. are presented in this report.

METHODS AND MATERIALS

STUDY AREA

During 1961, sampling was conducted at 11 stations (fig. 1) over an area of about 20,725 km.^{2} (8,000 square miles). During cruises at 3-week intervals, plankton hauls were made at stations where water depth was about 14, 27, 46, and 82 m.

SAMPLING GEAR AND CALIBRATION

Plankton samples were obtained with the Gulf-V plankton net described by Arnold (1959). This gear consists of a metal frame, to which a conical monel net with a mesh size of 31.5 strands per centimeter is attached. The diameter of the net mouth is about 40.5 cm. Plankton was collected in a cup attached to the end of the net. After each tow the net was thoroughly washed down and the plankton removed and preserved in 5 percent Formalin.[2]

Estimates of water volume filtered during each tow were calculated from a flowmeter positioned in the center of the net mouth. Both TSK and Atlas flowmeters, calibrated by the technique outlined by Ahlstrom (1948), were used. Each tow lasted 20 minutes, and towing speeds averaged 4.6 km. per hour (2.5 knots). Flowmeter readings indicated that during each tow the net filtered about 100 m.^{3} of water. Catches are reported in numbers of organisms per 100 m.^{3} of water strained.

DEPTHS FISHED AND TOWING CABLE PROFILE

Each of four depths was fished for 5 minutes during each tow: 3 m. above the bottom, two intermediate depths, and 3 m. below the surface. The two intermediate depths fished were equally spaced vertically within the water column and depended on the total water depth. Sampling depths were determined by the trigonometric function of the wire angle and length of towing cable. Realizing that this technique assumed the profile of the towing cable to be a straight line, we attached a bathykymograph [3] (Model T-1a, Marine Advisors, Inc.) to a Gulf-V net and made tests to determine the reliability of this technique. Results are given in table 1.

A plot of mean actual depths vs. calculated depths provides an estimate of the error between the actual and assumed towing cable profiles (fig. 2). Agreement was close to a

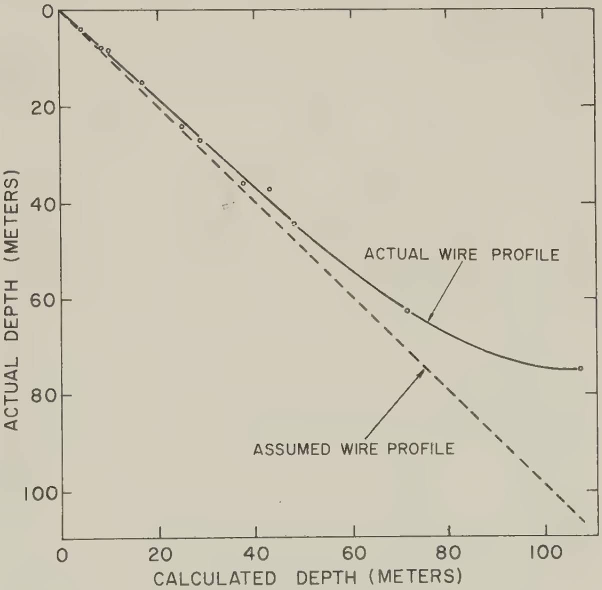

FIGURE 2.—The calculated and actual profiles of the towing cable attached to a Gulf-V plankton net.

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[2] Trade names referred to in this publication do not imply endorsement of commercial products.

[3] Calibration accuracy ± 1 percent full scale. Sensitivity 0.5 percent of full scale.

TABLE 1.—*Results of tests to determine reliability of calculated sampling depths attained by using wire angle and length of towing cable*

Observations	Calculated depth	Average actual depth	Range of observed depths
Number	*Meters*	*Meters*	*Meters*
5	3	3	2–4
1	5	4	–
1	8	7	–
7	10	8	4–10
16	17	17	8–22
16	25	24	17–35
10	29	27	24–32
3	38	36	25–48
10	43	37	32–45
10	48	44	35–57
13	71	63	55–77
3	107	75	64–88

depth of 50 m., but became progressively poorer beyond this depth. Consequently, the deepest samples from stations in 82 m. of water probably were taken at a distance above the bottom that averaged considerably greater than the intended 3 m.

DAY VS. NIGHT CATCHES OF PLANKTONIC-STAGE *PENAEUS SPP.*

The oblique-step tow was used throughout this study in an attempt to eliminate possible differences in day and night catches caused by diurnal migrations of larval shrimp. Russell (1925, 1928) has shown that, in general, decapod larvae undergo diurnal vertical migrations. More recently Temple and Fischer (1965) observed similar migrations in planktonic stages of penaeid shrimp in the northwestern Gulf of Mexico when temperature profiles (bathythermograph traces) indicated a stratified water column.

Hydrographic conditions over the Continental Shelf in the northwestern Gulf of Mexico appear to be seasonal, as there are definite times when temperatures of the waters are either stratified or isothermal (Harrington, 1965). The time and extent of these seasons vary, however, depending on total water depth and to some degree on distance offshore. In general, water is stratified at a total depth of 14 and 27 m. during May to July, at 46 m. during May to September, and at 82 m. during April to October. In other months, temperatures are essentially isothermal.

Average day and night catches were calculated for stations at which water was stratified and for those at which the water column was isothermal (table 2). Hauls with no shrimp were excluded. Catches made at the 82-m. stations also were excluded because no larvae appeared to be present during either the day or night at certain times of the year, and water deeper than 50 m. was not sampled adequately. After a test of homogeneity indicated a need for logarithmic transformation of the data, statistical treatment revealed that day and night catches did not differ significantly during either stratified or isothermal conditions. As used in this study, the oblique-step tow apparently did prevent possible differences in day and night catches caused by diurnal migrations of larval shrimp.

TABLE 2.—*T-test of average catches of planktonic-stage Penaeus spp. in day and night samples during different temperature conditions in the northwestern Gulf of Mexico, 1961*

[Number per 100 $m.^3$ of water strained]

Stage	Water stratified			Water isothermal		
	Day	Night	"t"[1]	Day	Night	"t"[1]
Nauplius	12.5	10.0	0.468	24.1	14.5	0.948
Protozoea	67.2	42.7	.314	28.0	54.7	.515
Mysis	22.2	11.7	.673	13.8	12.3	.263
Postlarva	.0	7.3	--------	15.4	12.6	.345
All stages	64.5	19.2	1.214	41.7	38.8	.092

[1] "t" value at .05 level.

ASSOCIATED PHYSICAL DATA

In addition to the plankton sampling at each station, temperature and salinity measurements were taken with a Foxboro Dynalog at selected depths. Temperatures were recorded to 0.1° C. and salinities to 0.1 p.p.t. (parts per thousand).

LABORATORY PROCEDURES

In the laboratory, plankton samples were transferred from 32-fluid-ounce (9.6 dl.) jars to 8-fluid-ounce (2.4 dl.) jars, and the 5 percent Formalin solution was replaced by a new 5 percent solution with glycerin and borax added. Each sample was examined under a microscope at magnifications that ranged from 0.7X to 6.0X. All planktonic stages of penaeids were removed, sorted to developmental stage, identified to genus, and counted. Postlarvae of the genus *Penaeus* were measured and identified to species by using characteristics described by Baxter and Renfro (1967).

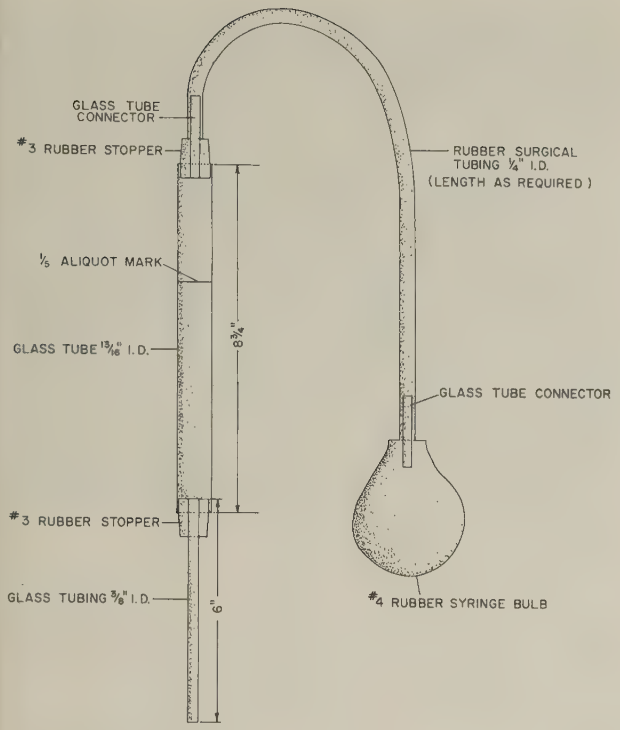

Figure 3.—Syringe device used for subsampling plankton.

The amount of each sample examined depended on the settled volume of plankton. Hauls in which the settled volume was less than 25 ml. were examined in their entirety; when sample volume exceeded 25 ml., only one-fifth of the total sample was examined. Aliquots were extracted directly from the samples with a syringe device (fig. 3). Subsampling accuracy was checked by applying chi-square tests to pooled counts from aliquot sizes ranging from one-fifth to four-fifths of the total sample (table 3). These tests indicated that the subsampling technique provided adequate estimates of total counts.

TRENDS IN SEASONAL ABUNDANCE AND THEIR IMPLICATIONS

Seasonal trends in abundance for all planktonic stages of *Penaeus* spp. were determined for 14-, 27-, 46-, and 82-m. stations (table 4). Cumulative yearly totals showed that the greatest catch per unit of effort for each stage was made at the 46-m. stations.

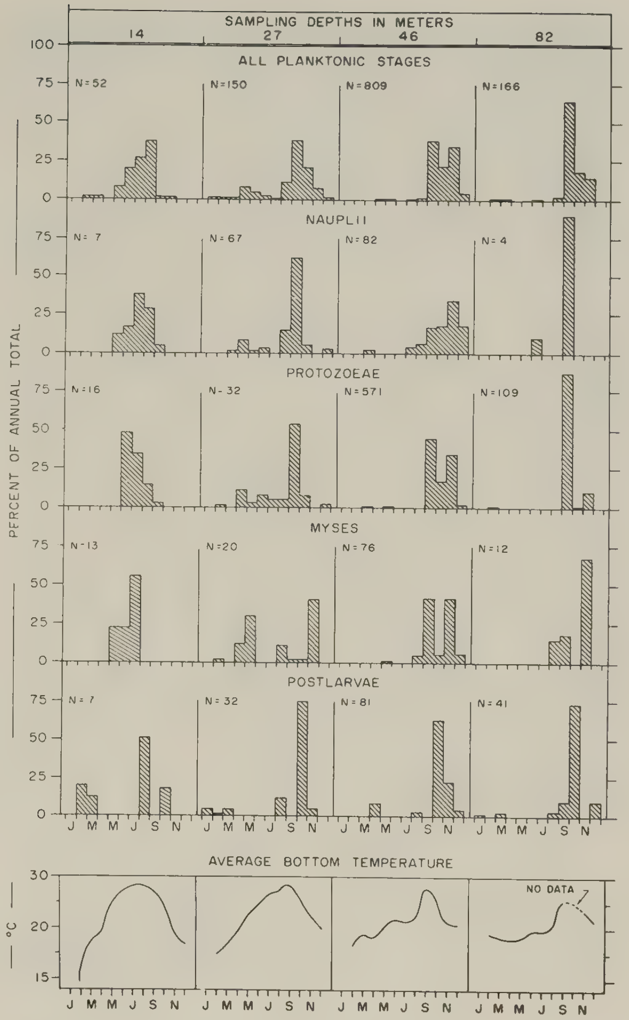

Figure 4.—Seasonal abundance trends of planktonic-stage *Penaeus* spp. and average bottom temperature by station depths in 1961.

Distinct trends in abundance for all planktonic stages combined were evident at each of the four depths (fig. 4). Two peaks of abundance were evident at each depth, but abundance was always much greater during the second peak. The time of greatest abundance was during May to August in 14 m. of water, August to November in 27 m., and September to November in 46 and 82 m. In general, peak abundance was attained at a progressively later time in the year with an increase in water depth. In addition, observed increases in abundance and increases in temperature of bottom waters at each depth were closely parallel, suggesting a possible direct relation.

At the 27-, 46-, and 82-m. stations, larval stages, excluding postlarvae, were taken in

TABLE 3.—*Results of tests to determine subsampling accuracy for obtaining total counts of larval shrimp in plankton samples*

Larvae in sample	Fraction of sample examined							
	One-fifth		Two-fifths		Three-fifths		Four-fifths	
	Samples tested	Chi-square value	Samples tested	Chi-square value	Samples tested	Chi-square value	Samples tested	Chi-square value
Number	*Number*		*Number*		*Number*		*Number*	
1-10	7	[1]6.155	5	0.630	2	0.060	2	1.841
11-49	22	.156	7	.070	3	.205	2	.033
50-99	9	.312	5	.090	4	1.370	4	.027
100-199	10	2.056	8	.873	8	.005	6	.986
200-299	3	1.488	2	3.195	2	2.111	2	[1]4.380
600-699	1	.010	1	1.145				
900-999	1	.385	1	.132	1	.312	1	1.204

[1] Significant at .05 level; chi-square table value = 3.841.

plankton hauls during both periods of increased abundance. At 14-m. stations, however, larval stages were encountered only during May to September. Postlarval stages made up the entire catch in February and March. Exclusion of postlarvae from the catches, consequently, results in a unimodal trend in larval abundance at the shallowest stations and a bimodal trend at deeper stations.

The difference between depths in timing of peak larval abundance is believed caused by the bathymetric distribution of the white and brown shrimp, which constitute about 98 percent of the total commercial shrimp landings from this area. Lindner and Anderson (1956), reporting on the bathymetric distribution of white shrimp in Louisiana and Texas waters, indicated that although a few adults may be in water deeper than 27 m., the bulk of the population is in shallower water. The spawning period in May to August, indicated by the occurrence of larvae in our plankton hauls at 14- and 27-m. stations, agrees closely with the spawning season of white shrimp along the Louisiana and Texas coasts postulated by Lindner and Anderson (1956).

Periods of increased larval abundance measured at 27-, 46-, and 82-m. stations reflect, we believe, the spawning activity of brown shrimp. The bathymetric distribution of adult brown shrimp along the Texas and Louisiana coasts can be inferred from the statistics of commercial landings supplied by the U.S. Fish and Wildlife Service. These data reveal that although brown shrimp concentrations vary seasonally, the greatest number of adults usually are in water 27 to 46 m. deep during the fall. In addition, Renfro and Brusher (manuscript in preparation), [4] who determined

TABLE 4.—*Monthly catch of Penaeus spp. by depth, 1961*

[Number of shrimp per 100 m.^{3} of water filtered]

Depth and planktonic stage	Month												Cumulative total
	January	February	March	April	May	June	July	August	September	October	November	December	
14 meters:													
All stages	0.0	1.4	0.7	0.0	4.4	10.5	13.9	18.6	1.0	1.2	0.0	0.0	51.7
Nauplii	.0	.0	.0	.0	2.2	2.9	6.5	4.7	.6	.0	.0	.0	16.9
Protozoeae	.0	.0	.0	.0	.0	7.6	5.2	2.3	.4	.0	.0	.0	15.5
Myses	.0	.0	.0	.0	2.2	.0	2.2	8.1	.0	.0	.0	.0	12.5
Postlarvae	.0	1.4	.7	.0	.0	.0	.0	3.5	.0	1.2	.0	.0	6.8
27 meters:													
All stages	1.3	.9	2.1	11.6	7.8	4.5	1.9	17.9	59.2	31.0	9.8	2.2	150.2
Nauplii	.0	.0	.7	5.8	1.0	1.9	.0	10.2	41.9	4.3	.0	1.1	66.9
Protozoeae	.0	.3	.0	3.3	.9	2.6	1.9	1.8	16.9	2.7	.0	1.1	31.5
Myses	.0	.3	.0	2.5	5.9	.0	.0	2.2	.4	.5	8.2	.0	20.0
Postlarvae	1.3	.3	1.4	.0	.0	.0	.0	3.7	.0	23.5	1.6	.0	31.8
46 meters:													
All stages	.0	.0	3.3	6.3	3.6	.0	3.3	11.8	303.9	166.6	278.2	31.9	808.9
Nauplii	.0	.0	2.6	.0	.0	.0	3.3	4.7	13.7	14.5	28.2	14.6	81.6
Protozoeae	.0	.0	.7	.0	2.4	.0	.0	1.2	258.3	97.8	200.7	9.4	570.5
Myses	.0	.0	.0	.0	1.2	.0	.0	3.5	31.9	3.6	31.7	4.2	76.1
Postlarvae	.0	.0	.0	6.3	.0	.0	.0	2.4	.0	50.7	17.6	3.7	80.7
82 meters:													
All stages	.0	1.3	.9	.0	.0	.4	.0	3.1	105.1	30.9	24.4	.0	166.1
Nauplii	.0	.0	.0	.0	.0	.4	.0	.0	3.4	.0	.0	.0	3.8
Protozoeae	.0	.9	.0	.0	.0	.0	.0	.0	95.4	.5	12.2	.0	109.0
Myses	.0	.0	.0	.0	.0	.0	.0	1.7	2.1	.0	8.1	.0	11.9
Postlarvae	.0	.4	.9	.0	.0	.0	.0	1.4	4.2	30.4	4.1	.0	41.4
Cumulative total—all stages	1.3	3.6	7.0	17.9	15.8	15.4	19.1	51.4	469.2	229.7	312.4	34.1	

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[4] "Seasonal abundance, size distribution, and spawning of penaeid shrimp in the northwestern Gulf of Mexico," by William C. Renfro and Harold A. Brusher, Bureau of Commercial Fisheries Biological Laboratory, Galveston, Tex.

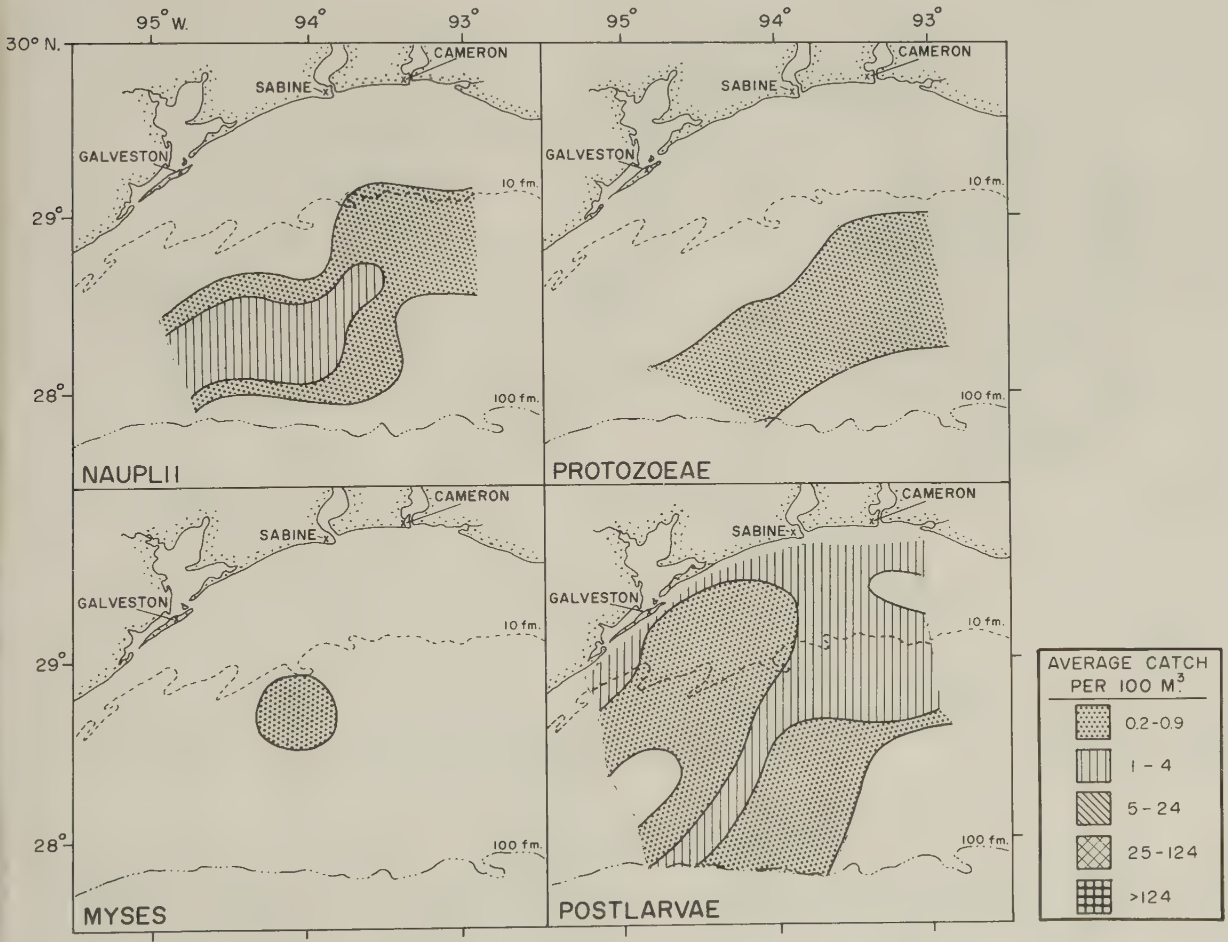
spawning seasons of the brown shrimp by ovarian examination, reported that ripe brown shrimp rarely occur in water less than 27 m. deep along the Texas and Louisiana coasts.

SPAWNING IN RELATION TO BOTTOM TEMPERATURES

Because penaeids are poikilothermic and larval abundance is apparently related directly to seasonal warming of bottom waters, we considered the possibility that spawning, indicated by the presence of naupliar stages in plankton hauls, might occur over a rather narrow temperature range. The yearly range in bottom temperatures decreased with an increase in depth. At the shallowest stations, temperatures ranged from 5.9° to 30.4° C., and at the deepest stations, from 16.8° to 26.2° C. In general, naupliar stages occurred over a temperature range of 17.0° to 28.5° C., but the magnitude of the range varied between depths (table 5). At 14-, 27-, 46-, and 82-m. stations the magnitude of the range where nauplii were taken was 3.8°, 11.5°, 8.5°, and 5.6° C., respectively.

DISTRIBUTION OF PLANKTONIC-STAGE SHRIMP

Areal distribution charts for each planktonic stage were made for January to March, April to August, and September to December. Values plotted at each station were obtained by averaging catches per 100 $cm.^3$ of water filtered for


95° W.
94°
93°
95°
94°
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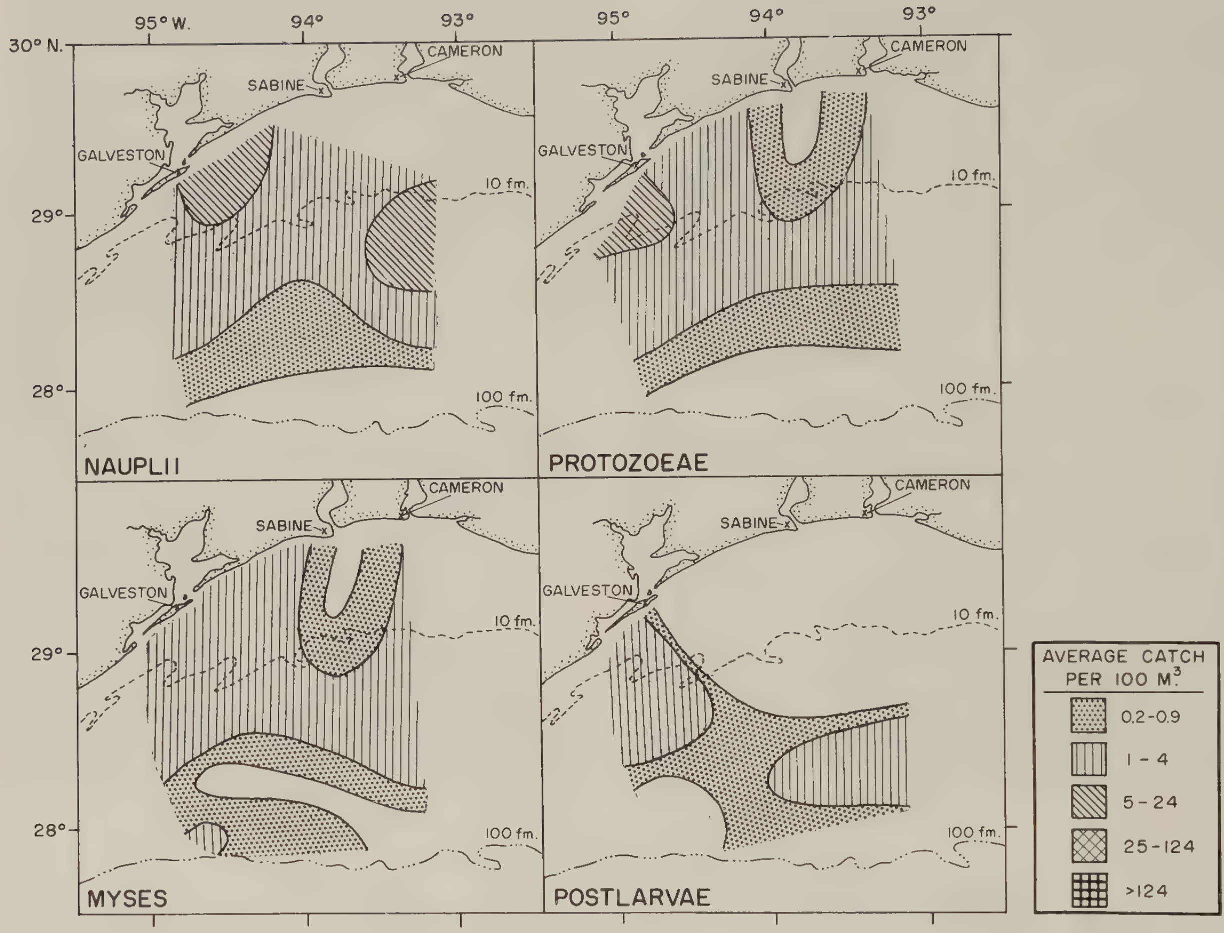
30° N.
29°
28°
29°
28°
CAMERON
SABINE
GALVESTON
10 fm.
100 fm.
NAUPLII
PROTOZOEAE
MYSES
POSTLARVAE
AVERAGE CATCH PER 100 M³
0.2-0.9
1 - 4
5 - 24
25 - 124
>124

FIGURE 5.—Relative abundance and distribution of planktonic-stage *Penaeus* spp., January to March 1961.


95° W.
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NAUPLII
PROTOZOEAE
MYSES
POSTLARVAE
AVERAGE CATCH PER 100 M.³
0.2-0.9
1 - 4
5 - 24
25 - 124
>124

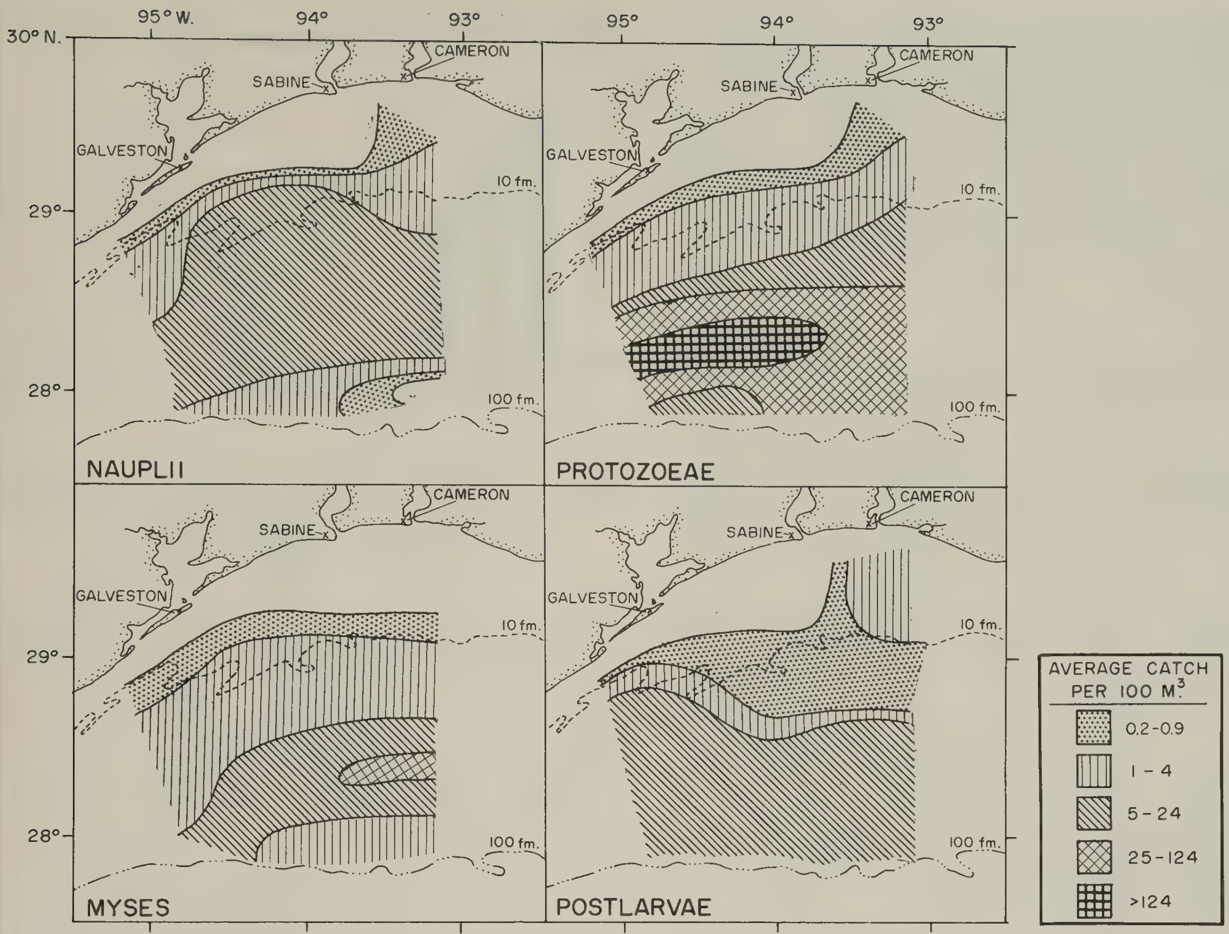
FIGURE 6.—Relative abundance and distribution of planktonic-stage *Penaeus* spp., April to August 1961.

TABLE 5. —*Yearly range in bottom temperatures and temperatures in which naupliar stages were taken in the northwestern Gulf of Mexico in 1961*

Station depth	Yearly range in temperature	Temperature in which nauplii occurred	
		Range	Magnitude of range
Meters	*° Centigrade*	*° Centigrade*	*° Centigrade*
14	5.9–30.4	24.7–28.5	3.8
27	11.9–31.0	17.0–28.5	11.5
46	14.2–27.7	19.0–27.5	8.5
82	16.8–26.2	19.9–25.5	5.6

each time period. Isopleths were then drawn to delineate areas of planktonic-stage concentrations (figs. 5, 6, and 7).

Slight shifts in the areal distribution of naupliar, protozoeal, and mysis stages were apparent. In January to March, larvae were restricted largely to waters deeper than 14 m. and shallower than 82 m.; in April to August concentrations were primarily shoreward of 46 m.; and in September to December, when the great-


95° W.
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30° N.
29°
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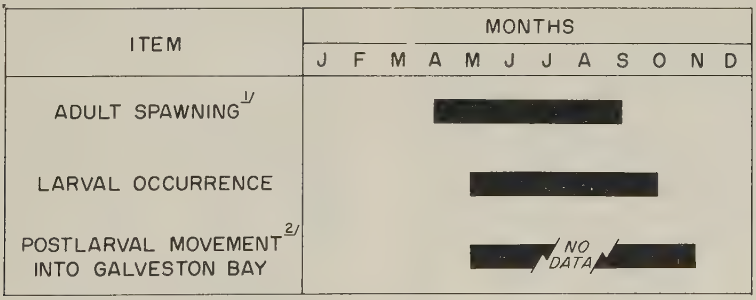
29°
28°
CAMERON
SABINE
GALVESTON
10 fm.
100 fm.
NAUPLII
PROTOZOEAE
MYSES
POSTLARVAE
AVERAGE CATCH PER 100 M.^{3}
0.2-0.9
1 - 4
5 - 24
25 - 124
>124

FIGURE 7.—Relative abundance and distribution of planktonic-stage *Penaeus* spp., September to December 1961.



1/TAKEN FROM LINDNER AND ANDERSON, 1956
2/TAKEN FROM BAXTER AND RENFRO, 1966

FIGURE 8.—Months of spawning, larval occurrence, and postlarval movement into Galveston Bay by the white shrimp, *P. setiferus*.

est number of larvae were caught, they were restricted generally to waters deeper than 14 m. The occurrence of larvae at 14-m. stations in April to August reflects, we believe, the spawning of white shrimp in shallow waters. Similarly, increased concentrations of larvae from September to December in deeper waters indicate the spawning of brown shrimp.

The areal distribution of postlarvae during the three periods differed from that of larvae.

Postlarvae occurred throughout the area in January to March, but when abundance and areal distribution of larvae were increasing in April to August, postlarval catches were generally low and postlarvae were not as widely distributed as larvae. During the ensuing months, however, the distribution of postlarvae increased, and in September to December it closely approximated that of the larval stages.

ABUNDANCE OF LARVAE AND POSTLARVAE IN RELATION TO SPAWNING PERIODS AND POSSIBLE OVERWINTERING

Although species differentiation of the larval stages of *Penaeus* spp. is impossible at this time, we have hypothesized that trends in larval abundance observed in different depths of water are the result of differences in depth and season of spawning of white and brown shrimp. The hypothesis that greatest abundance of larvae at the shallowest stations (14 m.) follows the spawning of white shrimp is compatible with the works of Pearson (1939) and Lindner and Anderson (1956). In addition, since larval development requires 2 to 3 weeks (Pearson, 1939), agreement is also close between larval occurrence at 14-m. stations and postlarval movement of white shrimp into Galveston Bay reported by Baxter and Renfro (1967). Spawning, maximum larval abundance, and postlarval movement of white shrimp into the nursery areas are apparently completed over a 7- to 8-month period within a calendar year (fig. 8).

The chronology of spawning, larval abundance, and postlarval movement of brown shrimp into Galveston Bay is not as apparent as for white shrimp. Increasing abundance of larvae at station depths of 27 m. or deeper appears to follow closely the spawning of brown shrimp reported by Renfro and Brusher. (See footnote 4.) When compared with movement into Galveston Bay reported by Baxter (1963), however, a definite anomaly is apparent (fig. 9). Most postlarvae moved into the Bay in the spring, but the largest catches of larvae in the Gulf were made in the fall. Because similar trends in larval abundance (Fischer, 1966) and postlarval movements (Baxter and Renfro, 1967) have been observed in recent years, the possibility that techniques of sampling bias the results appears to be negligible.

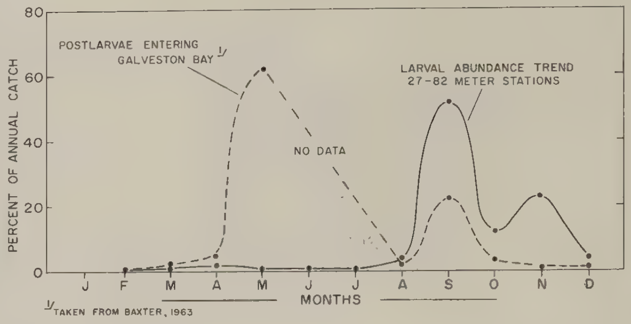


FIGURE 9.—Larval abundance trends in 27 to 82 m. of water adjacent to Galveston and postlarval movement of brown shrimp into Galveston Bay, 1961.

The difference in timing between offshore larval and inshore postlarval peaks can possibly be explained by examining seasonal abundance trends and length-frequency distributions of postlarval brown shrimp taken in plankton hauls. Postlarvae were generally taken in plankton hauls from January through April, and August through December (fig. 4). As with larvae, most postlarvae were taken in the fall. Length-frequency distributions, based on total lengths from the tip of the rostrum to the tip of the telson, reveal two distinctly different size groups (fig. 10). In January to April, most postlarvae averaged 11 to 12 mm., whereas in August to December they averaged only 6 to 7 mm.

The size difference between the two groups of postlarvae has significance when compared with length-frequency distribution of postlarvae migrating into Galveston Bay (Baxter and Renfro, 1967). Postlarval shrimp taken during the peak inshore movement average about 12 to 13 mm. in total length, and were probably represented offshore by the group of postlarvae averaging 11 to 12 mm. taken between January and April. The question still remains, however: From what spawning and peak of larval abundance did the postlarvae originate? Kutkuhn (1966) stated that the postlarvae probably originated from ". . . heightened spawning activity in offshore brown shrimp populations during February and

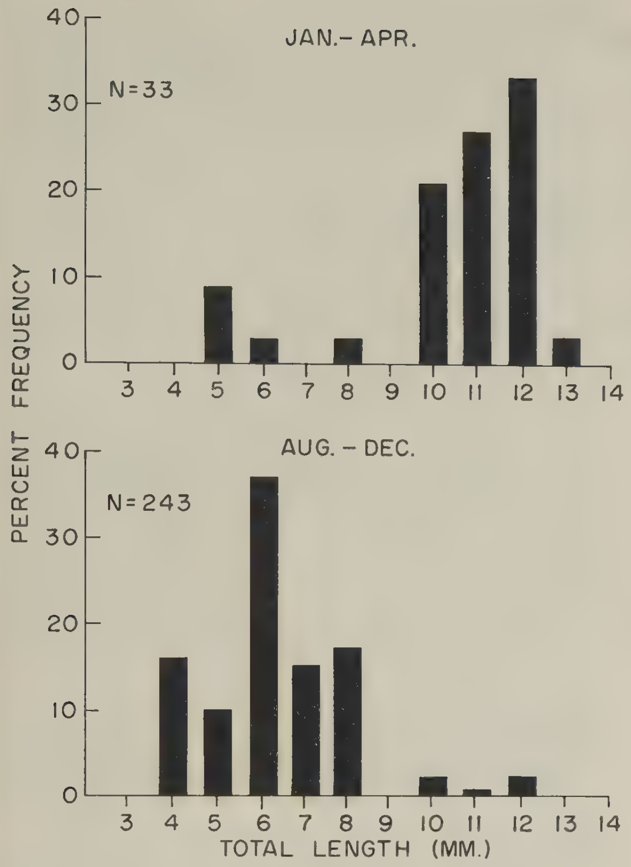


FIGURE 10.—Length-frequency distributions of postlarval brown shrimp (*P. aztecus*) taken in plankton hauls, 1961.

March. . ." Renfro and Brusher (see footnote 4), however, reported that, although brown shrimp may spawn continually throughout the year, major periods of spawning activity are in April to June and September to November. Furthermore, in the absence of large catches of larval stages during January to March 1961, the possibility arises that this spring group of postlarvae originated from a large spawning in the fall of 1960. If this is true, young brown shrimp must remain offshore either as larvae or postlarvae for a longer period than was previously suspected.

If young brown shrimp do overwinter offshore, the developmental rate of these larvae or the growth rate of the postlarvae, or both, must be slower than has been previously reported for white shrimp. Cook (1966 b), while rearing larval brown shrimp, observed retarded developmental rates at temperatures lower than 30° C. Zein-Eldin and Aldrich (1965) reported that postlarvae held in the laboratory under controlled temperature had a maximum growth rate of about 1.4 mm. per day at 32° C. and 1.1 mm. per day at 25° C. They also found that growth of postlarvae held over a 30-day period at 11° C. was practically nil, but that survival was high.

Additional support for the hypothesis that brown shrimp may overwinter before entering the nursery areas was provided by Aldrich, Wood, and Baxter.[5] They found that in the laboratory postlarval brown shrimp would burrow in response to experimentally reduced temperatures. This response usually occurred between 12° to 17° C. It appears then that under certain temperatures postlarval brown shrimp may burrow and grow at a slow rate.

Results of laboratory experiments on larval development rates, postlarval growth, and postlarval burrowing characteristics are of particular significance because temperatures similar to those tested occur in the waters over the Continental Shelf of the northwestern Gulf of Mexico (Harrington, 1965). Of even greater significance is the fact that these temperatures occur between the fall peak of larval abundance (apparently associated with brown shrimp spawning) and the peak occurrence of postlarval brown shrimp in Galveston Entrance. Additional field and laboratory work is required, however, to substantiate the hypothesis of overwintering brown shrimp larvae or postlarvae, or both, in offshore waters.

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[5] "A behavioral comparison of postlarval *Penaeus aztecus* and *P. setiferus*, with regard to burrowing as a response to reduced temperatures," by David V. Aldrich, Carl E. Wood, and Kenneth N. Baxter, Bureau of Commercial Fisheries Biological Laboratory, Galveston, Tex., 3 figs.

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PRINCIPAL DISEASES OF COMMERCIALLY IMPORTANT MARINE BIVALVE MOLLUSCA AND CRUSTACEA

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ABSTRACT

Diseases of commercially important marine bivalve mollusks and crustaceans can cause mortalities in natural and captive populations. Oysters have suffered frequent and extensive mass mortalities. Epizootic disease has sometimes been indicated, as for example in "dermocystidium disease," caused by a fungus, in the Gulf of Mexico, and "Delaware Bay disease," caused by a protozoan, in the Middle Atlantic States. Fungus organisms have also been implicated in "shell disease" of European oysters and a fatal disease of bivalve larvae in hatcheries. Several species of haplosporidan Protozoa cause serious mortalities of oysters and mussels. Larger animal parasites, such as larval trematodes and parasitic copepods, can affect reproduction, growth, and survival of bivalve mollusks.

Diseases of crustaceans are usually less well known. Effects of pathogens are most apparent in captive populations, where mortalities may result from outbreaks of microbial agents. Lobsters have two known bacterial diseases: the often very lethal "gaffkaemia" which occurs in wild populations, but severely affects impounded stocks; and "shell disease," caused by chitin-destroying bacteria, which is important in captive populations, probably by interfering with respiration of infected individuals. Mortalities of captive blue crabs have also been attributed to possible respiratory impairment caused by ciliate gill associates. Microsporidan Protozoa can be important parasites of crabs and shrimps; depending on their habitat within the host, they may destroy muscle tissue or gonads and have been postulated as causes of mortality. Among the larger parasites of crustaceans, rhizocephalan barnacles have long been known to cause degeneration of gonads in crabs of many species.

The described pathogens of commercial invertebrate species probably constitute only a small percentage of the many disease agents that affect marine populations. Many mass mortalities have been described in the literature; disease has been implicated in some of them, but the etiologic agent rarely has been determined precisely, and the relative importance of other environmental factors has been assessed infrequently. Diseases and parasites can also exert significant "background" effects such as continued low-level mortality, depressed reproductive capacity, and increased susceptibility to predation.

Disease control measures are possible and have been applied to a few populations of sedentary inshore marine invertebrates. Possible methods of control include quarantine, selective breeding of disease-resistant strains of shellfish, environmental manipulation (dredging of growing areas, chemical treatments, control of density of planting, and scheduled harvest), and more extensive use of artificial environments such as hatcheries and artificial ponds.

As understanding of factors that influence the numbers of animals in the sea has expanded, it has become evident that disease, among other environmental variables, can drastically affect abundance. This fact has been clearly demonstrated in populations of sedentary inshore invertebrates. Many marine invertebrate species, harvested in great numbers, constitute marine crops of high value. Some, such as mussels, oysters, clams, crabs, lobsters, and shrimps, occur in inshore or estuarine waters, and have been cultivated in varying degrees in different parts of the world. Under natural conditions or under cultivation, mass mortalities occasionally occur; here disease can be an important contributing factor.

The word "disease," as used in this paper, includes abnormalities resulting from microbial pathogens or parasite invasion, and tumors. Not included are genetically or environmentally induced abnormalities, or physiological disturbances not related to an infectious agent or parasite. For each host group considered in this review a sequence of diseases, beginning

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with those caused by bacteria (virus diseases, with but a single exception (Vago, 1966), have not been identified in marine invertebrates) and progressing to fungi, protozoans, and larger parasites, has been followed. Often a host species may be infected by several well-defined pathogens, as well as assorted parasites that have variable impact on the host population. The common and the scientific names of parasites and hosts are usually both given when the organisms are first mentioned in the text, after that either one may be used.

No general review has been made of the literature on diseases of marine invertebrates (Steinhaus, 1965), but particular groups—especially those of commercial importance—have received some attention. Dollfus (1921a), Pelseneer (1928), Ranson (1936), and Fischer (1951) have summarized information about the parasites and diseases of mollusks—particularly oysters—and Hutton, Sogandares-Bernal, Eldred, Ingle, and Woodburn (1959) reported on parasites and diseases of some of the commercial shrimps. Certain general aspects of invertebrate diseases, such as immune mechanisms, have been considered (Cantacuzène, 1923, 1928; Huff, 1940; Baer, 1944; Steinhaus, 1949; Stauber, 1961), and a few research groups, such as Frederik B. Bang and his associates at The Johns Hopkins University, and Albert K. Sparks and his co-workers at the University of Washington, have been concerned with comparative pathology of invertebrates (Bang, 1956, 1961, 1962; Bang and Bang, 1962; Bang and Lemma, 1962; Levin and Bang, 1964; Rabin and Bang, 1964; Sparks and Pauley, 1964; Pauley and Sparks, 1965).

Much of our knowledge about diseases of marine invertebrates concerns species of economic importance, particularly the bivalve molluscan and crustacean shellfish. This paper is concerned only with the important diseases of these two groups. We have attempted to encompass as much literature as possible from widely separated areas. Many diseases of marine invertebrates are inadequately characterized, and it is probable that others have not even been recognized. Microbial pathogens that have been implicated in mass mortalities include bacteria, fungi, and protozoans. Several of the larger parasites have been found to be pathogenic under specific conditions. Not included here are most of the parasites and diseases of noncommercial species—those species that may be of great significance in the cycles of life in the sea, but which are not of significant direct importance as food for humans. Among the groups thus excluded are gastropods and cephalopods, barnacles, copepods, and most of the smaller crabs. Also excluded are many diseases that have been incompletely described in the scientific literature.

A summarization of knowledge in any area of research, however specialized in its scope, is subjective and in some ways frustrating to the reviewer; yet a consolidation of research results can be useful, particularly to the nonspecialist. Much published information about diseases of marine bivalve mollusks and crustaceans has accumulated, and at least a representative fraction of the available literature has been considered in this paper. Preparation of a bibliography of molluscan shellfish diseases has been a continuing project of the BCF (Bureau of Commercial Fisheries) Biological Laboratory, Oxford, Md., for 6 years; this bibliography, as well as standard bibliographic and abstracting sources, has been used in preparing the manuscript. There is little representation of the Russian literature—this may be in part a reflection of the relative lack of emphasis placed on shellfish in Russian fishery research, as well as the limited availability of translations of Russian literature. Some of the older European literature, particularly that on specific parasites of invertebrates, has not been considered in this paper but is accessible through references cited in more recent publications. Although necessarily limited in content, this review attempts to assess the state of knowledge about the role of disease in two major groups of commercial marine invertebrates.

DISEASES OF BIVALVE MOLLUSCA

Most of the commercial bivalve mollusks occur in shallow inshore waters, often intertidally, where they are accessible to quantitative evaluation and observation. Unusual mortalities are more apparent here than in offshore populations. As a result, literature on mass mortalities of species such as oysters and mussels is voluminous. Disease has sometimes been demonstrated to be the cause of deaths; in other situations, disease has been strongly suspected, or the cause has not been determined. Within the past decade knowledge about molluscan shellfish diseases has increased at a greatly accelerated pace, largely because of concern about mortalities which have occurred in widely scattered populations. Literature on oyster diseases is most abundant; that on mussel and clam diseases is less voluminous.

OYSTERS

The 20th century has been a difficult and troublesome period for oysters (family Ostreidae) in many parts of the world (Orton, 1924a; Roughley, 1926; Gross and Smyth, 1946; Logie, 1956; Mackin, 1961; Sindermann, 1966c). Decline in abundance of oysters actually started late in the 19th century, probably caused in large part by indiscriminate harvesting and destruction of beds. Extensive mortalities from unknown causes also contributed to decreased oyster production. The rate of decline on the North American east coast and in other geographic areas has recently increased because of large-scale mortalities, several of which have been caused by disease. Largely because of their worldwide economic importance, oysters are among the most thoroughly studied of marine animals—especially their diseases and parasites. Interest in oyster diseases has logically arisen from catastrophic mortalities in many parts of the world. Many unsolved problems remain but the body of literature is large, and is growing rapidly.

Among the important diseases of oysters are microbial diseases and those caused by helminths and parasitic crustaceans.

Microbial Diseases

Bacteria, fungi, and protozoans are the principal causes of microbial diseases in oysters.

Bacteria.—Reports of mass mortalities of Pacific oysters, *Crassostrea gigas* (Thunberg), have been published recently in Japan (Fujita, Matsubara, Hirokawa, and Araki, 1953, 1955; Takeuchi, Takemoto, and Matsubara, 1960; Ogasawara, Kobayashi, Okamoto, Furukawa, Hisaoka, and Nogami, 1962; Imai, Numachi, Oizumi, and Sato, 1965; Kan-no, Sasaki, Sakurai, Watanabe, and Suzuki, 1965; Mori, Imai, Toyoshima, and Usuki, 1965; Mori, Tamate, Imai, and Itikawa, 1965; Numachi, Oizumi, Sato, and Imai, 1965; Tamate, Numachi, Mori, Itikawa, and Imai, 1965). Takeuchi et al. (1960) implicated a gram-negative, motile, 1– to 3–μ bacillus, probably an *Achromobacter*, in large-scale mortalities in Pacific oyster culture areas of Hiroshima Bay since 1946. Experimental infections were achieved with cultured bacteria, but the organisms could be isolated from healthy as well as sick oysters, and from sea water. Moribund oysters had diffuse cell infiltration, massive increase in bacterial numbers, and tissue necrosis.

Numachi et al. (1965) found up to 20 percent infection with gram-positive bacteria (not further identified) in oysters during mass mortalities in Matsushima Bay, Japan, in the early 1960's. The disease was called "multiple abscesses," but the authors did not think that a causal relation existed between bacteria and mortalities. A similar disease was found in 1965 by staff members of the BCF Biological Laboratory, Oxford, Md., in seed oysters (less than 1 year old) imported to the U.S. west coast from Matsushima Bay, and in adult oysters from Willapa Bay, Wash. The disease has been labeled "focal necrosis" (fig. 1). Studies of the etiologic agent and its pathogenicity

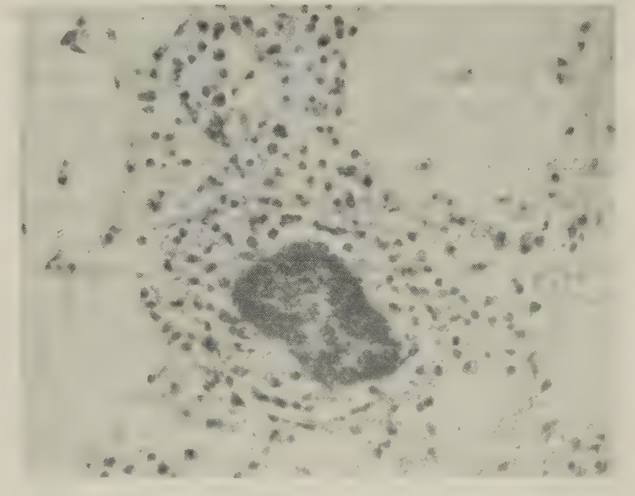

FIGURE 1.—"Focal necrosis" in connective tissue of Pacific oyster from Willapa Bay, Wash., surrounded by extensive leucocytic infiltration (× 700).

are in progress. The disease affects seed oysters as young as 6 months, as well as adults. The necrotic foci or multiple abscesses may represent the resistant or arrested disease state, and the active, fulminating phase may have already killed susceptible members of the population.

Several bacterial pathogens of bivalve larvae have been isolated (Guillard, 1959; Tubiash, Chanley, and Leifson, 1965). Identified only as *Aeromonas* sp. or *Vibrio* sp., the organisms killed larvae and juveniles of five bivalve species tested, including American oysters, *Crassostrea virginica* (Gmelin), and European oysters, *Ostrea edulis* L., but did not affect adults.

Fungi.—Oysters have several fungus diseases, some of serious consequence. Identification of fungus pathogens, especially in the early literature, has often been tentative, and only a few adequate characterizations of etiologic agents have been made.

A relatively well-known fungus infecting oysters from the Atlantic and Gulf coasts of the United States is *Dermocystidium marinum.* First described by Mackin, Owen, and Collier (1950), the pathogen has been the subject of much research. A useful diagnostic technique, based on antibiotic fortified fluid thioglycollate medium, was devised by Ray (1952, 1966b) during attempts to culture the organism. A number of authors have shown that *D. marinum* causes oyster mortalities (Mackin et al., 1950; Mackin, 1953; Andrews and Hewatt, 1954; Hewatt and Andrews, 1954; Ray, 1954a, 1954b, 1954c). Pathological changes in infected oysters were described by Mackin (1951). Invasion takes place through the gut epithelium and possibly through the mantle. The epithelium is destroyed; the parasite lyses the basement membrane and is distributed by the blood to all parts of the body (fig. 2). All tissues are invaded and damaged, and multiple abscesses are formed. Normal gonad development is inhibited, infected oysters become severely emaciated (Ray, Mackin, and Boswell, 1953; Ray, 1954b), and growth is retarded (Menzel and Hopkins, 1955b).

Temperature is important in the epizootiology of dermocystidium disease (Hewatt and Andrews, 1956). Infections and associated mortalities rise during the warmer months and decline during colder periods. Mortalities decline in winter, probably because of reduced parasite metabolism, rather than elimination of the organism. Failure to find *D. marinum* consistently north of Chesapeake Bay suggests that prolonged low temperature may be a significant limiting factor. Andrews (1965) found that *D. marinum* proliferates readily only at temperatures above 25° C., and overwinters as subpatent infections. His further observation, that the partial destruction of oyster populations by a protozoan disease resulted in decreased prevalence of the fungus organism, suggests that *Dermocystidium* is dependent upon direct transmission from one oyster to another. Other evidence for direct transmission was provided by Ray and Mackin (1955).

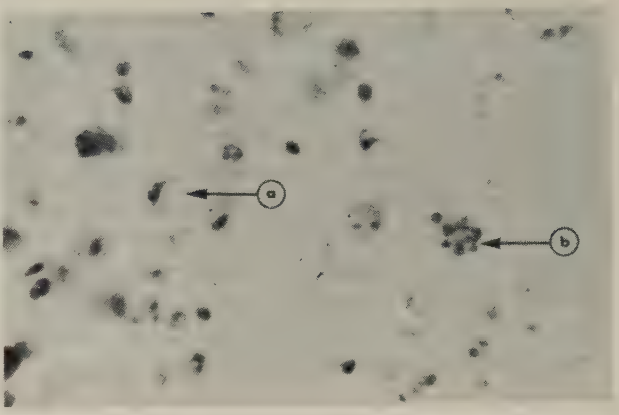

FIGURE 2.—Dermocystidium disease of American oysters. Histologic section of infected oyster showing diagnostic "hypnospore" (a) and "rosette" (b) (× 1,000).

Infections and resulting mortalities are reduced in salinities below 15 o/oo. Ray (1954b) found evidence that low salinity retarded development of terminal infections in laboratory populations. Ray and Chandler (1955) suggested that excessively high salinities may also be unfavorable for *Dermocystidium.* Mackin (1956) found a positive correlation between high salinity and high incidence of the fungus, but he observed that the salinity tolerance range was wide in experimental studies. Dilution of infective elements by inflow of fresh water was suggested as an important limiting factor and a possible control measure.

D. marinum is abundant in waters of the southern United States. Ray (1966a) who surveyed the occurrence of the fungus in the Gulf of Mexico in 1961 and 1962, found infections in 35 of 39 oyster samples, and prevalences as high as 100 percent. Hoese (1964) was able to find *D. marinum* in the digestive tracts and feces of fish, oyster drills, and crabs that had fed on dying and dead infected oysters. He speculated that transmission of the fungus might be furthered by scavengers and that scavengers may release the parasite from host tissue.

D. marinum is common in oysters from most high-salinity areas of the South Atlantic and Gulf of Mexico coasts of the United States, but is absent in a few such areas. Hoese (1963) attempted assays of water samples from different coastal locations in one section of the Texas coast to determine their inhibitory effects on development of fungus hypnospores. Although results were not conclusive, water samples from certain localities apparently stopped hypnospore development. Hoese speculated that the absence of *D. marinum* may be related to those *Spartina* salt marshes where consistently high salinities occur.

In addition to its common occurrence in *C. virginica, Dermocystidium* has been found in other species. Ray (1954b) reported it in the leafy oyster, *Ostrea frons* L., from Florida and in horse oysters, *O. equestris* Say, from Texas. The organism was not found, however, in the mangrove oysters, *C. rhizophorae* (Guilding), from Puerto Rico, in *O. edulis* from Holland, or in the rock oyster, *C. commercialis* (Iredale and Roughley), from Australia. *O. lurida* (Carpenter), the Olympia oyster, was experimentally infected by exposure to infected *C. virginica. Dermocystidium*-like organisms have also been seen in other mollusks and annelids. Andrews (1955) found what he termed "*Dermocystidium*-like" organisms in 12 of 16 mollusk species from the Chesapeake Bay area.

This important fungus pathogen of oysters continues to be the subject of much research. Knowledge of its biology has been summarized by Ray (1954b), Ray and Chandler (1955), Andrews and Hewatt (1957), and Mackin (1962). Mackin and Boswell (1956) proposed a life cycle for *D. marinum* that included a saprophytic stage leading to production of an infective spore. Recently, Perkins and Menzel (1966) described motile biflagellate stages that were also postulated to be infective to oysters. Mackin and Ray (1966) grew the organism on beef-serum agar plates and suggested that it belongs in the genus *Labyrinthomyxa,* a member of the Labyrinthulales. Culture of a *Dermocystidium* similar to *D. marinum* in chemically defined medium (Goldstein, Belsky, and Chasak, 1965) should make possible the study of isolates from many areas to determine whether one species or a species complex exists, and should permit more precise determination of the taxonomic affinities of the *Dermocystidium* group of protistan parasites.

Korringa (1947, 1951a, 1951c) reported that mortalities of the European oyster in Holland, beginning in 1930, were caused by a fungus disease characterized by formation of green or brown pustules on the inner shell surfaces. Activity of the fungus varied directly with temperature, and the outbreak was said to be intensified by widespread use of cockle shells as spat collectors. Thin parts of oyster shells were perforated by the disease agent, which proliferated after reaching the interior surfaces. The fungus had been identified earlier as a species of *Monilia* by Voisin (1931), who found the infection, called "shell disease," in 40 percent of oysters imported into France from Holland in 1931. Cole (1950) and Cole and Waugh (1956) found infections in the European oyster from Brittany and in Portuguese oysters, *C. angulata* (Lamarck), grown in England. Infections were common in beds where old shells were abundant. Cole and Hancock (1956) found the disease in almost all beds of native European oysters, and described two distinct forms: the typical one characterized by greenish rubbery warts and knobs on the inside of the shell, particularly in the region of the muscle attachment; and an atypical form in which young oysters had thickened shells with numerous white patches but had no deformation of the muscle attachment area.

Another disease of the European oyster, which may be identical to shell disease, has been misnamed "foot disease" or "maladie du pied" (Dollfus, 1921a). It has long been known on the coast of France; Giard (1894) described its etiologic agent as a bacterium, *Myotomus ostrearum*, but further definitive studies of the causative organism are needed. The disease is localized in the shell under the attachment of the adductor muscle, where it causes roughening and blistering of the shell and degeneration of adjacent muscle tissue. The muscle may become detached as irregular cysts are formed. Major mortalities occurred on oyster beds at Arcachon, France, in 1877 (Hornell, 1910; Orton, 1937). The cause was not determined, but some evidence of "foot disease" was found. Galtsoff (1964) reported the rare occurrence of the disease in the American oyster from the southern United States, but did not consider it a serious threat to oyster populations. Durve and Bal (1960) reported the rare occurrence of a shell disease which they considered to be "maladie du pied" in the backwater oyster, *C. gryphoides* (Schlotheim) from India.

Davis, Loosanoff, Weston, and Martin (1954) isolated a fungus, later described as *Sirolpidium zoophthorum* (Vishniac, 1955), from hatchery-produced oyster and clam larvae. The infections were rare, but they produced occasional epizootics that killed most of the cultured larval population in 2 to 4 days. Juvenile as well as larval bivalves were infected; growth ceased and death followed soon after infection. Infected cultures of bivalve larvae contained large numbers of motile biflagellate zoospores of the fungus. The authors speculated that an epizootic of the fungus could occur among lamellibranch larvae in nature.

There are several inconclusive reports of organisms resembling actinomycetes in oysters. Eyre (1924) reported *Cladothrix dichotoma* from oysters examined during the great mortalities of 1919–23 in western Europe. The isolate was not pathogenic in experimental studies. Dollfus (1921a) stated that Eyre's isolate was a species of *Nocardia*. Pettit (1921) also identified a *Nocardia* from *O. edulis*, but Dollfus (1921b) considered this to be merely normal cell reticulum of the oyster. Mackin (1962) described a "mycelial disease" of *Crassostrea virginica*, which he thought might be caused by an actinomycete. We have recently seen an organism similar to that described by Mackin in *C. angulata* from France.

Protozoa.—A variety of Protozoa parasitize oysters (Rosenfield, 1964; Sindermann, 1966b), and certain Sporozoa[1] are serious pathogens. Two haplosporidans, *Minchinia costalis* (Wood and Andrews) and *M. nelsoni* Haskin, Stauber, and Mackin, have caused oyster mortalities on the North American east coast within the past decade (fig. 3).

M. costalis is found in seaside bays of Maryland and Virginia, along the lower eastern shore of Virginia, and in Delaware Bay (Andrews, Wood, and Hoese, 1962; Wood and Andrews, 1962; Sprague, 1963; Haskin, Stauber, and Mackin, 1966; Couch, 1967b). First recognized in moribund and dead oysters from Hog Island Bay, Va., in 1959 by Wood and Andrews, *M. costalis* was held responsible, on the basis of epizootiological evidence, for sharp peaks of mortality in early summer. The pathogen and mortalities caused by it continue to characterize Maryland and Virginia seaside oyster populations.

The second haplosporidan species, *M. nelsoni*, has a wider distribution—from Connecticut to North Carolina. It has caused extensive mortalities and drastic decline of the oyster fishery in Delaware Bay beginning about 1957 and in lower Chesapeake Bay beginning in 1959 (Mackin, 1960; Engle and Rosenfield, 1963; Andrews, 1964). In each affected area, mortalities have often exceeded 95 percent for several years. Because of the severe impact of the *M. nelsoni* epizootic on oyster stocks of the Middle Atlantic States, a number of research groups—university, State, and Federal—have participated in scientific studies since the late 1950's, and significant papers have been published recently. Haskin et al. (1966) named the plasmodial stage of the parasite as *Minchinia nelsoni;* Couch, Farley, and Rosenfield (1966) associated the plasmodium with spore and prespore stages; and Barrow and Taylor (1966) confirmed, with immunological techniques, the association of plasmodium and spore. Andrews (1964, 1966) described aspects of the epizootiology of the disease in Virginia waters, and Haskin, Canzonier, and Myhre (1965) briefly summarized the epizootiology in Delaware Bay.

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[1] Throughout this paper an attempt has been made to conform to the revised classification of the Protozoa as proposed by Honigberg, Balamuth, Bovee, Corliss, Gojdics, Hall, Kudo, Levine, Loeblich, Weiser, and Wenrich (1964), and modified by Sprague (1966a).

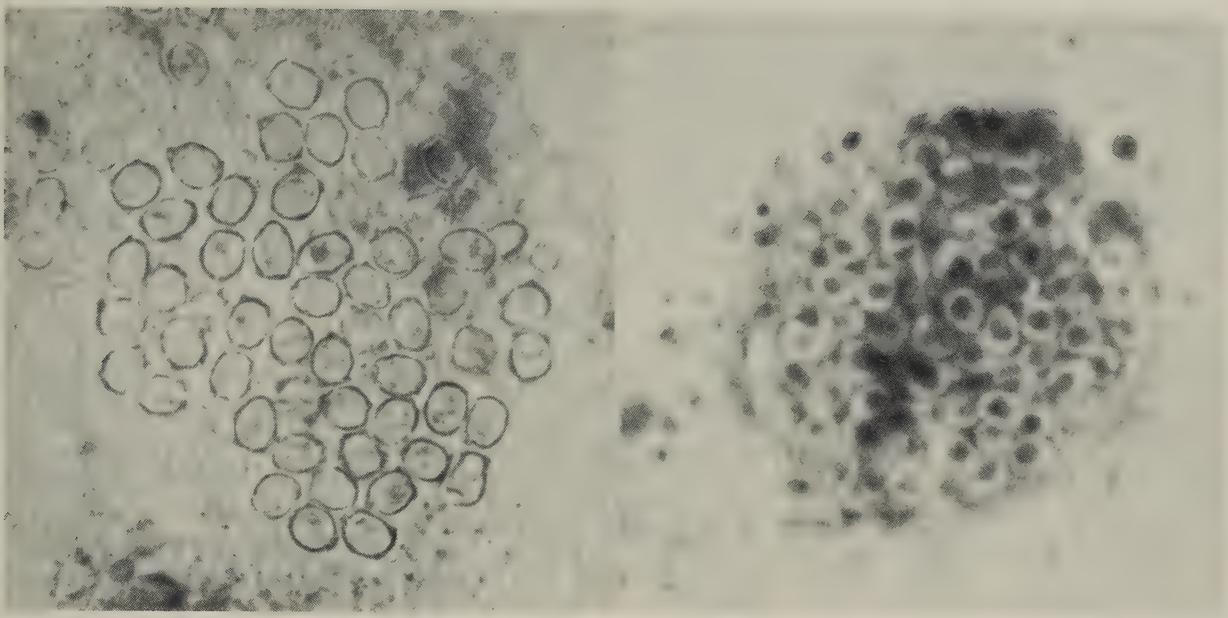

FIGURE 3.—Sporocysts of *Minchinia nelsoni* (formerly known as "MSX"), the etiolic agent of "Delaware Bay disease" in an American oyster—fresh preparation at left, and stained section at right (× 1,000).

Farley (1965), after completing a 5-year histopathological study of Chesapeake Bay oysters, categorized natural infections according to extent of invasion and nature of host response.

As an example of the effects of *M. nelsoni* on the U.S. oyster fishery, landings in New Jersey waters of Delaware Bay in the late 1940's and early 1950's had fluctuated around 6 million pounds of shucked meats until the mid-1950's, when disease decimated the stocks. Landings fell precipitously to a low of 167,000 pounds in 1960, and no significant recovery has occurred (fig. 4). Comparable effects have been felt in the high-salinity waters of lower Chesapeake Bay, another major oyster producing area.

Thus far, one alleviating influence seems to be salinity. *M. nelsoni* occurs in waters whose salinity consistently exceeds 15 o/oo; during 3 years (1963–65) of drought along the Atlantic coast, the pathogen invaded areas of middle Chesapeake Bay formerly free of the disease (Rosenfield and Sindermann, 1966). Temperature may also be important, since the pathogen appears to be quiescent during the winter.

Although several life history stages have been recognized for both species of *Minchinia*, and concurrent infections have been found (Couch, 1967b), routes of infection and methods of transmission are still unknown. Because several research groups are actively concerned with oyster diseases on the U.S. east coast, particularly with *M. nelsoni,* increased understanding of this and other pathogens should develop rapidly. Recently, we have seen in Pacific oysters from Taiwan plasmodial parasites morphologically very similar to those found in American oysters.

Léger and Hollande (1917) described another haplosporidan, *Chytridiopsis ovicola,* infecting the eggs of European oysters taken at Marennes, France. The parasite was relatively rare and occurred only in certain ovarian follicles of parasitized oysters.

Nematopsis ostrearum Prytherch, a gregarine parasite of the American oyster, was held (Prytherch, 1938, 1940) to be the cause of extensive mortalities in Virginia and Louisiana. Later studies (Sprague, 1949; Sprague and Orr, 1955) indicated, however, that *Nematopsis* did not cause deaths of oysters and suggested that *Dermocystidium* infections may have complicated earlier results. Owen, Walters, and Bregan (1952) found no correlation between *Nematopsis* infections and oyster mor-

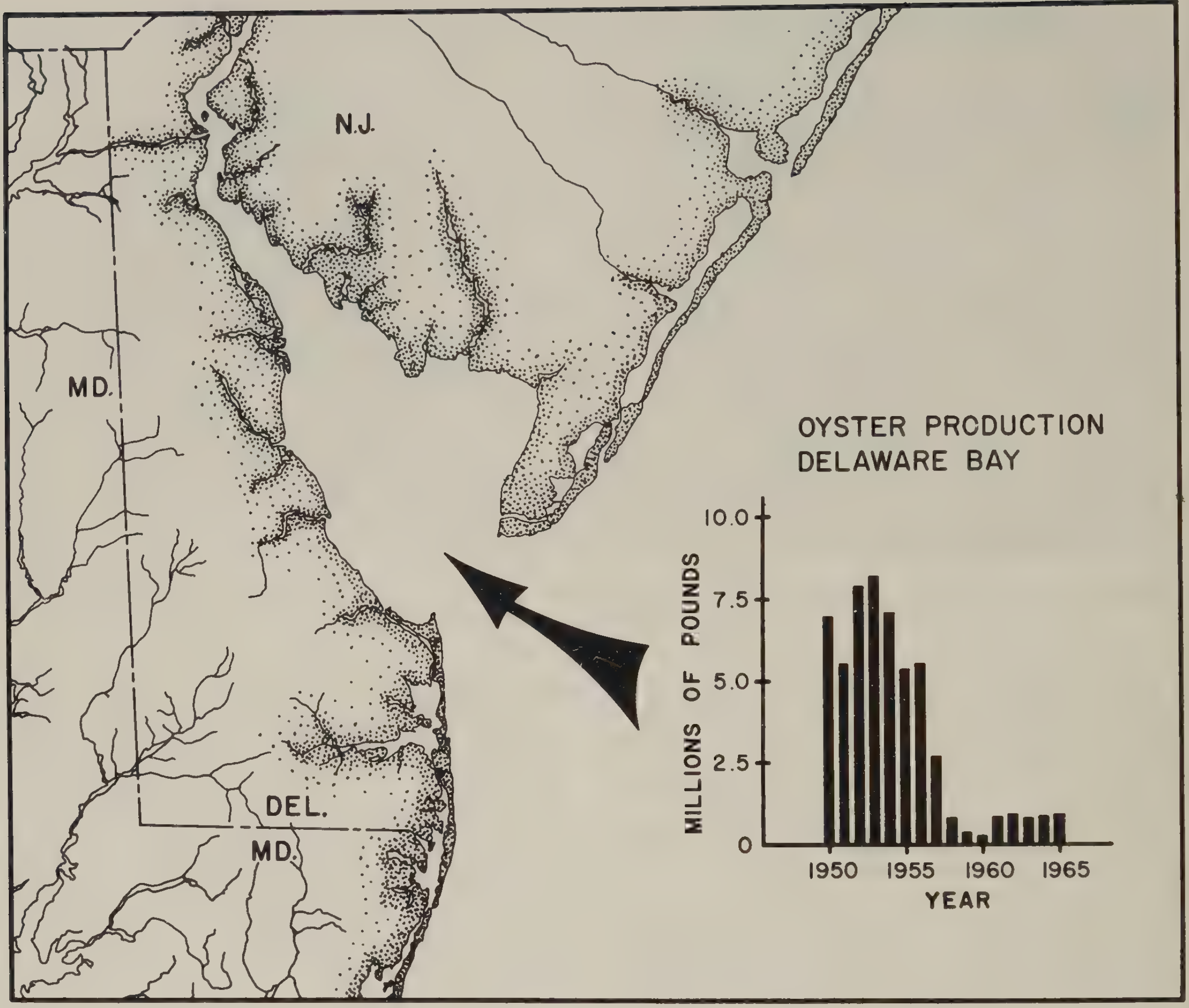

FIGURE 4.—Oyster production in New Jersey waters of Delaware Bay, 1950–65.

talities in Louisiana. Sprague and Orr (1953, 1955) demonstrated that *N. ostrearum* as described by Prytherch, was actually two species, which they designated *N. ostrearum* (emended) and *N. prytherchi*. Spores of *N. prytherchi* are larger and more elongate, localize in the gills rather than in the mantle, and have vegetative stages only in the crab *Menippe mercenaria* (Say). The life cycle of *N. ostrearum* includes a mud crab host—*Panopeus herbstii* Milne-Edwards, *Eurypanopeus depressus* (Smith), or *Eurytium limosum* (Say). In many oyster-growing areas most oysters are infected, although infections are rarely heavy. Mackin (1962) has pointed out the lack of tissue reaction to the parasite and the lack of evidence for existence of lysins or toxins. Feng (1958) found that a dynamic equilibrium existed between acquisition by the oyster of new parasites and elimination of spores.

Nematopsis was found to be widely distributed on the Atlantic and Gulf coasts of the United States by Landau and Galtsoff (1951). They found heavy infections in oysters from certain localities, such as the mouth of Chesapeake Bay, but relations with other ecological factors such as abundance of crabs were not apparent. The intensity of infection was cumulative and increased with age of the host. No evidence was obtained to indicate that *Nematopsis* infection caused poor meats or mortality of oysters.

Hexamita sp., a flagellate protozoan, occurs frequently in the digestive tract of oysters, but its parasitic or saprozoic role has not been adequately determined. First described by Certes (1882) as a commensal in European oysters, the flagellate was later held responsible for oyster mortalities from "pit disease" in Holland (Mackin, Korringa, and Hopkins, 1952). Clear evidence of pathological effects was not obtained, and heavy bacterial infections further complicated the study. *Hexamita* was also blamed for mortalities of Olympia oysters in the State of Washington (Stein, Denison, and Mackin, 1961), but again clear evidence of pathogenicity was not presented. Scheltema (1962), who examined the relation between *Hexamita* and American oysters from Delaware Bay, concluded that the organism did not contribute significantly to deaths of oysters. He suggested, as did Stein et al. (1961), that *Hexamita* may act as a pathogen during periods of low environmental temperatures and low host metabolism but that prevalence declines at higher temperatures because the processes in oysters which act to remove the trophozoites exceed the reproductive rate of the flagellate. We have recently seen *Hexamita* in Pacific oysters from Korea and Taiwan.

Several ciliate parasites have been described from American oysters. A member of the genus *Sphenophrya* was reported by the BCF Biological Laboratory, Oxford, Md. (Anonymous, 1965), as the cause of an oyster disease characterized by formation of large cysts on the gills. Richardson[2] and Laird (1961) identified ciliates in the gut of *C. virginica* from Prince Edward Island, Canada, as *Orchitophrya stellarum* Cépède. Prevalence was low, but infections were heavy and the intestinal epithelium had been invaded. *O. stellarum* is known as a serious pathogen of starfish, in which it causes gonad destruction (Cépède, 1911; Smith, 1936; Vevers, 1951). Laird speculated that the organism may be a regular and possibly harmful parasite of oysters and that starfish may become infected from them.

Mackin (1962) mentioned a ciliate parasite of oysters from the Atlantic and Gulf coasts of the United States, which he considered to be *Ancistrocoma pelseneeri*, a well-known parasite of mussels. The ciliates were abundant in the digestive tracts of oysters infected with *Dermocystidium marinum*, but Mackin did not believe that they were pathogenic to the oyster host.

Two amebae are known from American oysters. Hogue (1914, 1921) described *Vahlkampfia calkensi* and *V. patuxent*, which are parasitic in the digestive tract. She distinguished the two species on the basis of differences in the cyst wall. No evidence of pathogenicity was found, nor were these forms demonstrated to be other than saprozoic. Additional ameboid organisms isolated from American oysters were reported briefly by Sawyer (1966).

Diseases caused by Helminths

Both trematodes and cestodes parasitize oysters.

Trematodes.—European and American oysters are parasitized by larval trematodes of the genus *Bucephalus*. *B. haimeanus* was first reported by Lacaze-Duthiers (1854) from European oysters in the Mediterranean Sea, and *B. cuculus* was described by McCrady (1874) in American oysters from South Carolina. Sporocysts occur in the gonad and digestive gland of the oyster (fig. 5), and sterilize the host. The tentative life cycle of the parasite (Tennent, 1906) includes minnows (Cyprinidae) or mullets (Mugilidae) as second intermediate hosts, and gars (Lepisosteidae) as definitive hosts. Hopkins (1954, 1957b) reported parasitization of more than one-third of the oyster population in localized areas of the United States, although prevalence generally was much lower, particularly in open waters. Menzel and Hopkins (1955a, 1955b) suggested that early infections temporarily stimulate growth of the oyster, but that older infections retard growth. Hopkins (1957b) made the interesting, if somewhat facetious, observation that *Bucephalus* might be considered a gastronomically beneficial parasite in southern waters, since infected oysters have an excellent flavor and are fat-looking and glycogen-rich throughout the year, whereas normal oysters are spawned out, thin, and relatively tasteless during part of the year.

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[2] Data provided in Fisheries Research Board of Canada, Manuscript Report Series (Biology), mimeographed, unnumbered, 1939, "Report on the studies of eastern coast oysters during the season of 1939," by L. R. Richardson.

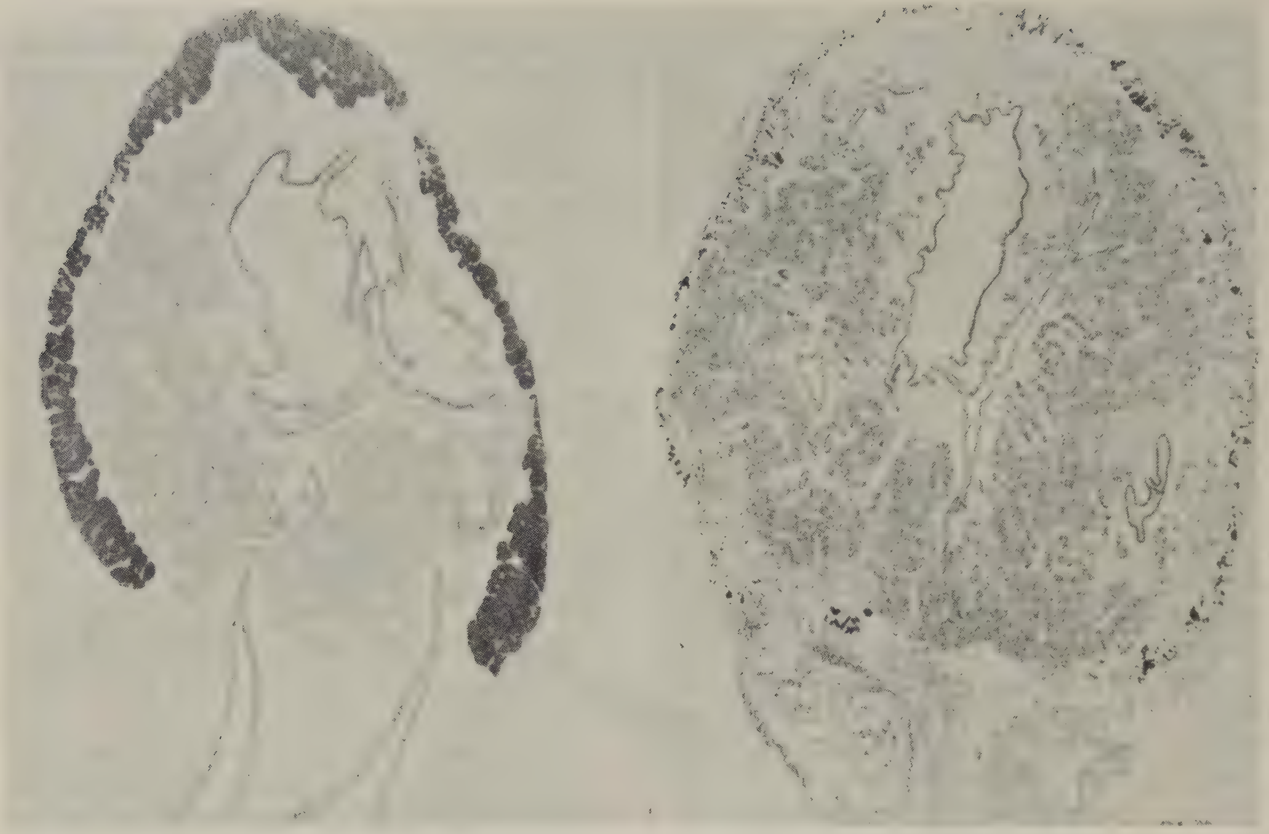

Figure 5.—Histological sections of oysters: (a) normal, and (b) parasitized by *Bucephalus* (× 3.5). Note in (b) the almost complete destruction of gonad tissue, which stains darkly in (a).

Recently, Cheng (1965) and Cheng and Burton (1965) used histochemical methods to examine the host-parasite relation of the American oyster and the larval trematode, *Bucephalus* sp. Parasitization caused marked changes in the distribution of fats.

Larval trematodes of the family Bucephalidae also occur in New Zealand oysters, *Ostrea lutaria* Hutton. Millar (1963) reported that oysters imported from New Zealand and maintained for breeding studies in Scotland were frequently parasitized and that the percentage mortality was much higher among parasitized individuals than among normal ones. We have recently found Pacific oysters from Taiwan to be infected with larval *Bucephalus*.

Hyperparasitization of sporocysts of *Bucephalus* in American oysters from the Gulf of Mexico was reported by Mackin and Loesch (1955). This hyperparasitization produced blackish discoloration of oyster mantle and viscera, and destruction of sporocysts, followed by release of the haplosporidan spores into host oyster tissue. Pronounced cellular reaction was elicited in the localized areas where spores were found in oyster tissue; the authors described some abnormal development of the hyperparasite in such tissue. The hyperparasite was not named, but it was considered on the basis of spore morphology to be a haplosporidan distinct from the parasite *Urosporidium pelseneeri* (Caullery and Chapellier) found in clams of the genus *Donax*.

Sprague (1964) described a microsporidan hyperparasite, *Nosema dollfusi*, of *Bucephalus* and speculated that escape of the protozoan into the tissues of the oyster could contribute to the death of the molluscan host. Shuster and

Hillman (1963) and Cheng (1964) made a similar speculation about haplosporidan hyperparasites of oysters.

Other larval trematodes occur on and in oysters. Fujita (1925, 1943) described *Gymnophalloides tokiensis*, a metacercaria which encysts, often in great numbers, on the mantle and gills. The host's physiology is disturbed, growth is halted, and reproduction is inhibited. Marine birds are definitive hosts for the parasite. Metacercariae of *Proctoeces ostrea* Fujita are also found in Japanese oysters. About 10 percent of the oysters in Hiroshima Bay were infected by the larval trematode, which localizes in gonad tissue. European oysters harbor the related *Proctoeces maculatus* Looss. Definitive hosts are labrid fishes in Europe, and snappers and red groupers, *Pagrosomus major* and *Epinephetus akaara,* in Japan.

Massive invasion by metacercariae in American oysters from the Texas coast was reported recently by Little, Hopkins, and Schlicht (1966). Feeding experiments showed that the trematodes were *Acanthoparyphium spinulosum* (Johnston), which matures in the intestine of shore birds. Most of the oysters examined had metacercariae in the mantle; the number averaged 45 worms per oyster.

Cestodes.—Oysters in several regions of the world are parasitized by larval cestodes of the genus *Tylocephalum.* These parasites are Lecanicephaloidea that occur as adults in the digestive tracts of elasmobranchs. Sparks (1963) reported heavy infections of *Tylocephalum* in American oysters introduced in Hawaii. In an addendum, Sparks noted that oysters from Florida had been reported by the BCF Biological Laboratory, Oxford, Md., to harbor similar larval cestodes (fig. 6). We have found similar larvae in oysters from Georgia and North Carolina. The coracidium of *Tylocephalum* was recently reported in the stomach and gills of American oysters collected at Pearl Harbor, Hawaii (Cheng, 1966). Penetration of gill or digestive epithelium was postulated from study of histologic sections. The pronounced cellular reaction in the subepithelial tissues—including encapsulation of the larvae—was described. Larval cestodes, probably *Tylocephalum,* have been found in Pacific oysters from Japan and Taiwan by staff members of the BCF Biological Laboratory, Oxford, Md. Members of this tapeworm group are known as parasites of pearl oysters in the Far East and were held to be the cause of pearl formation (Herdman, 1904; Herdman and Hornell, 1906; Shipley and Hornell, 1904, 1906; Southwell, 1924). Jameson (1912) presented convincing evidence, however, that invasion by larval trematodes, rather than larval cestodes, was more important in pearl development. Pearl formation around trematode and cestode larvae which invade the mantle and die appears to follow a similar pattern of host responses in bivalve mollusks (Wright, 1966).

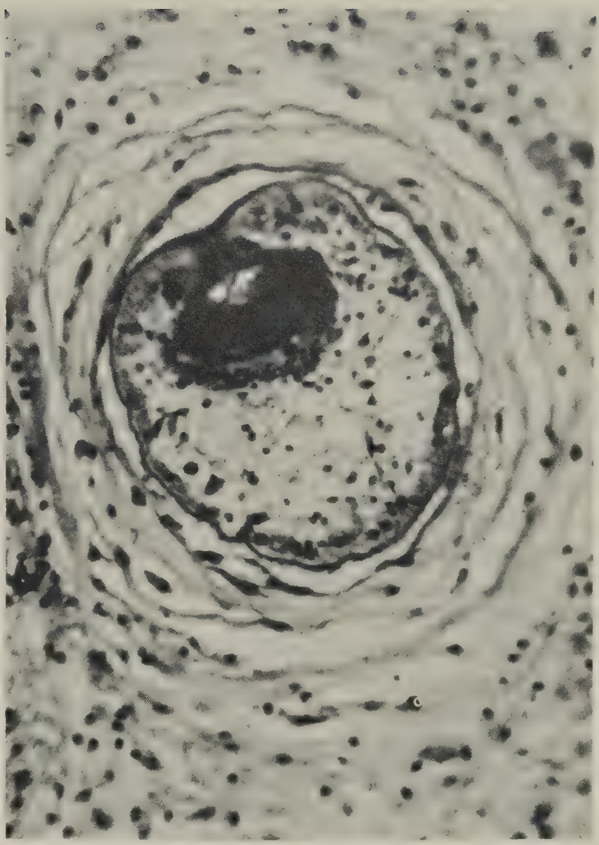

FIGURE 6.—*Tylocephalum* in American oyster from Apalachicola Bay, Fla. (× 70).

Diseases Caused by Parasitic Crustaceans

A parasitic copepod, *Mytilicola orientalis,* was described from the digestive tract of the Pacific oyster from Japan by Mori (1935). The parasite was transferred to the United States west coast with imports of seed oysters from Japan, and was described as *M. ostrea* by Wilson (1938), who was apparently unaware of Mori's report. Odlaug (1946) stated that Olympia oysters infected with even small numbers of *M. orientalis* had a lower condition index than uninfected oysters. Chew, Sparks, and Katkansky (1965) found a similar relation in Pacific oysters, and Sparks (1962) demonstrated pathological changes in gut epithelium and underlying tissues of these oysters infected with the copepod. Mori and Odlaug reported *M. orientalis* as a parasite of mussels (*Mytilus crassitesta* Lischke and *M. edulis* L.) as well as oysters, both in Japanese and United States waters. Another species, *Mytilicola intestinalis,* first described by Steuer (1902, 1903), has been blamed by Korringa (1950, 1959) and others for widespread mortalities of sea mussels, *Mytilus edulis,* in Europe but is found only rarely in European oysters (Baird, Bolster, and Cole, 1950; Hepper, 1953, 1956) and has not been reported to cause significant mortalities. A small specimen, identified as *Mytilicola intestinalis,* was found by Pearse and Wharton (1938) in an American oyster from the Florida coast. Humes (1954) believed that this copepod was probably *M. porrecta,* which he described from mussels and clams from Louisiana.

Crabs of the genus *Pinnotheres* occasionally inhabit the shell cavity of oysters, where their activities and effects suggest that they are parasites rather than commensals (Christensen and McDermott, 1958; Haven, 1959). Stauber (1945) studied a sudden increase in abundance of the oyster crab, *P. ostreum* (Say), in American oysters of Delaware Bay in 1941. He observed that the crabs robbed the oyster of food and injured the gills, resulting in a weakened condition of the host. Stauber found in 1941 that 90 percent of the oysters of Delaware Bay harbored four to six crabs in the first parasitic stage. He ascribed unusual mortalities in certain oyster populations to debilitation caused by high abundance of crabs. In 1942 abundance of crabs dropped to 25 to 30 percent, and continued to decline in following years.

Another *Pinnotheres* was described from Madagascar oysters, *Ostrea vitrifacta* Sowerby, by Poisson (1946); infestation was accompanied by development of a characteristic irritating flavor in the parasitized oyster. He speculated that this flavor might be traced in some way to the coelenterate *Sertularia,* which often grows on shells of oysters that contain *Pinnotheres.* Korringa (1952a) pointed out the striking similarity of this observation with the popular belief in Holland that eating mussels parasitized by *P. pisum* causes "nettle rash."

Tumors

Tumors in oysters have been reported. Benign mesenchymal tumors of pericardial origin have been described from oysters by Ryder (1887) and Smith (1934). The nodular, polypoid, pediculated growth found by Smith was over 3 cm. in greatest dimension. Sparks, Pauley, Bates, and Sayce (1964a) described a stalked mesenchymal tumor from the Pacific oyster that appeared to be histologically similar to that found by Smith. Sparks, Pauley, Bates, and Sayce (1964b) also reported a Pacific oyster with a tumorlike fecal impaction of unknown origin, accompanied by inflammation and encapsulation. The literature on tumors of other species of mollusks, as well as those of other invertebrates, has been reviewed by Scharrer and Lochhead (1950).

MUSSELS

Marine mussels, particularly *Mytilus edulis,* are abundant and palatable. They are grown by highly developed culture methods, especially in Western Europe. Culture of a single species, often under crowded conditions, however, increases vulnerability to disease. As with cultivated oysters, extensive and repeated mortalities, presumably caused by disease, have occurred in mussel beds. The parasitic copepod, *Mytilicola,* is the only specific pathogen that has been shown to cause mortalities in European mussels, although other parasites, particularly haplosporidan Protozoa and larval trematodes, have been reported.

Microbial Diseases

Eggs of the sea mussel from the western North Atlantic are occasionally infected with a haplosporidan, *Chytridiopsis mytilovum.* Field (1923) first described the parasite and several of its life history stages. Recently Sprague (1965b) has redescribed life history stages in more detail. The parasite has a high prevalence in some samples, although the proportion of infected eggs to normal eggs in any individual is low. Vincentiis and Renzoni (1963) recognized what seems to be the same organism in eggs of the Mediterranean edible mussel, *Mytilus galloprovincialis* L., from the Gulf of Naples. A similar parasite, *Chytridiopsis ovicola,* has been reported from eggs of the European oyster (Léger and Hollande, 1917).

Taylor (1966) described a disease of California mussels, *M. californianus* Conrad, caused by another haplosporidan, *Haplosporidium tumefacientis.* The disease, characterized by tumefactions of the digestive gland, was found in 23 of 1,114 individuals examined. The gross enlargement of the gland was apparently due to plasmodia of the parasite; no necrosis was reported. Samples of sea mussels collected simultaneously from the California coast by Taylor were not parasitized by the haplosporidan.

Sea mussels from the Baltic were found by Raabe (1934, 1936, 1938, 1949) to harbor a number of ciliates, including *Ancistrocoma pelseneeri* Chatton and Lwoff, *Kidderia mytili* (DeMorgan), *Ancistruma mytili* (Quennerstedt), and *Hypocomides mytili* (Chatton and Lwoff). The same species of ciliates have also been identified from *Mytilus* sampled in other geographic areas (Kidder, 1933; Chatton and Lwoff, 1934; Kozloff, 1946). Although many ciliates occur in bivalve Mollusca (Fenchel, 1965), a parasitic role has not been adequately determined for most of them.

Diseases Caused by Helminths

Invasion of mussels by larval trematodes is thought to be responsible in part for pearl formation. Jameson (1902) believed that most mussel pearls resulted from encystment of metacercariae and encapsulation by the host. Herdman (1904), who studied sea mussels in England, found pearls very common near Piel and attributed them to invasion by larvae of *Distomum (Gymnophallus) somateriae.*

The literature on trematode-induced pearl formation in mussels has been reviewed by Stunkard and Uzmann (1958). The relation between pearls in European sea mussels and trematode parasites was first described by Garner (1872), and later by Dubois (1901, 1903, 1907, 1909) who proposed the name *Distomum margaritarum (Gymnophallus margaritarum)* for parasites found in reddish-brown spots which served as foci for pearl formation in mussels from the French coast. Jameson (1902) stated that the larval trematodes resembled *D. somateriae* which had been described as an adult from the intestine of the eider duck, *Somateria mollissima,* by Levinsen (1881). Jameson referred the parasite to the genus *Lecithodendrium* Looss and described the process of pearl formation by the mantle of the mussel around the metacercariae. Giard (1903, 1907) confirmed these observations on pearl formation. Odhner (1905) designated the larvae causing pearl formation in mussels as *Gymnophallus bursicola.* Similar metacercariae were found by Stafford (1912) in mussels from the Gulf of Saint Lawrence. Jameson and Nicoll (1913) reviewed pearl formation in mussels and concluded that several gymnophallid larvae were involved. Since then other gymnophallid cercariae have been associated with metacercariae in mussels (Palombi, 1924; Cole, 1935; Rees, 1939). Stunkard and Uzmann (1958) fed mussels from Long Island to newly hatched eider ducks and recovered adult gymnophallids, probably *G. bursicola.*

Other larval trematodes have been described from mussels. Cole (1935) reported "orange sickness" of sea mussels at Conway in Wales. The color was due to masses of orange pigmented trematode sporocysts in the mantle and throughout the body; the tailless cercariae they contained were described as *Cercaria tenuans.* A similar condition had been noted previously by Atkins (1931a). Cole also described a second larval trematode infestation, caused by *Bucephalus mytili.* Uzmann (1953) found microcercous trematode larvae in sea mussels from Long Island and Connecticut that had a similar orange coloration. Described as *Cercaria milfordensis,* the larvae were primarily parasites of the blood vascular system of the host and had foci in the blood vessels of the mantle. Sporocyst development precluded normal gametogenesis in mussels; infected mussels held in aquaria had unusually high mortalities. Uzmann suggested that *C. milfordensis* infections are probably lethal to the host under unfavorable environmental conditions.

Diseases Caused by Parasitic Crustaceans

A well-documented example of the effects of disease on mussel populations is that of the invasion of the north European sea mussel stocks by the copepod *Mytilicola intestinalis.* A fascinating body of literature has accumulated about this parasite and its effects on mussels; only a sampling of the many published papers is cited here. Steuer (1902) first described the parasite from the intestines of Mediterranean edible mussels, and Pesta (1907) outlined the life history. Korringa (1950, 1959) described the relatively sudden appearance of *Mytilicola* in sea mussel stocks of the Netherlands in 1949 and its subsequent spread to many mussel beds during the following decade. The organism was known to occur in Mediterranean mussels since the beginning of the 20th century (Monod and Dollfus, 1932), and in 1938 was found near Cuxhaven, Germany, from whence it was assumed to have spread westward to the Netherlands. Spread was thought by Korringa and others to be aided by mussel encrusted ships, by movement of planktonic larvae, and by transfer of seed mussels from infested areas. *Mytilicola* was also very abundant in localized areas of the English coast in 1946. Korringa stated that the condition of mussels was generally correlated with intensity of parasitization; mussels with less than 5 copepods were still healthy, those with 5 to 10 were visibly thinner, and more heavily infested lots suffered serious mortalities. According to Meyer-Waarden and Mann (1954) and Mann (1956), gonad weights of infested individuals were 10 to 30 percent less than those of nonparasitized mussels.

There is some indication, however, that *M. intestinalis* exerts a less severe effect on populations of *Mytilus galloprovincialis* than on those of *M. edulis,* possibly because of its longer association with *M. galloprovincialis* and the consequent better adaptation of host and parasite—as was pointed out by Fleury, Lubet, and Le Dantec (1951). Hrs-Brenko (1964), for example, found no difference in condition index of parasitized and unparasitized mussels *(M. galloprovincialis)* on the Yugoslav Adriatic coast, and Genovese (1959) made similar findings on the Italian coast.

Infestation of sea mussels led to poor growth, thin meats (Cole and Savage, 1951; Mann, 1951), cream-colored rather than dark brown liver, failure of byssal development, and a dirty red-brown color. Reproduction of the parasite was accelerated by warm water, and the many young parasites present in the summer invaded and killed mussels. Deaths occurred among mussels of all sizes, including "seed." Mussels fell from culture racks and died during transport to markets (Brienne, 1964). Density of mussel beds was believed to directly influence survival and multiplication of the parasite. Infestations were light in areas where the mussels were thinly scattered and near the surface of the water. Because of the continued spread of *Mytilicola* in the Netherlands, an extensive scheme of repeated dredging of natural beds, transfer of lightly infested stocks, and destruction of heavily infested stocks was outlined by Korringa (1959) to create a barrier to further invasion.

Mytilicola in mussel populations grown on floats in Spain was studied by Andreu (1963). He found the infestation to be greater near shore where tidal currents were weak. Vertical distribution of the parasite in cultured mussels grown on 6–m. ropes was uniform in areas of strong currents but increased with depth where currents were weak. Such findings agree well with those of Hepper (1955), who concluded from field observations that mussels raised from the bottom, or in fast-moving water at either end of an estuary, were less heavily infested with *Mytilicola* than those on the bottom, in slow-moving water, or in the midregions of estuaries. Hepper felt that control of the copepod was possible by using off-bottom culture or by locating culture beds in fast-moving water or at the brackish-water ends of estuaries.

M. intestinalis, except for one doubtful North American record (Pearse and Wharton, 1938), is known only from Europe. It has been reported from Germany (Caspers, 1939; Meyer and Mann, 1950, 1952a, 1952b; Meyer-Waarden and Mann, 1956), the Netherlands (Korringa, 1951b, 1952b, 1953, 1957a), Belgium (Leloup, 1951, 1960), Scotland, England, and Ireland (Ellenby, 1947; Grainger, 1951; Hockley, 1952; Thomas, 1953; Bolster, 1954; Waugh, 1954), the north coast of France (Dollfus, 1914, 1927; Monod and Dollfus, 1932; Brienne, 1964), the northwest coast of Spain (Andreu, 1960, 1961, 1963), the Mediterranean Sea (Bassedas, 1950; Meyer-Waarden and Mann, 1953), and the Adriatic Sea (Steuer, 1902; Pesta, 1907; Meyer-Waarden and Mann, 1953). Waugh (1966) has mapped the recent distribution of the parasite in northern Europe. A conference to review and discuss problems of parasitization by *Mytilicola* was held in Paris, and the proceedings were published in 1951 (Cole, 1951a; Dollfus, 1951; Havinga, 1951; Heldt, 1951; Korringa, 1951b; Korringa and Lambert, 1951; Lambert, 1951a, 1951b; Leloup, 1951; Meyer and Mann, 1951). It was agreed that *Mytilicola* constituted a severe threat to the mussel industry of Europe, but whether the copepod was a direct or indirect cause of death was left undecided. Continuing mortalities associated with the presence of *Mytilicola* (Brienne, 1964), however, indicate a causal relationship, possibly influenced by stresses of spawning, high temperatures, and inadequate food supply.

Another species, *Mytilicola porrecta* Humes, occurs in ribbed and recurved mussels (*Modiolus demissus* Sowerby and *Mytilus recurvus* Rafinesque) in the Gulf of Mexico. Humes (1954) found as many as 15 individuals per mussel, but no pathology or mortality was indicated. A third species, *Mytilicola orientalis*, known to occur in *Mytilus edulis* and *M. crassitesta*, was recently reported from the California mussel by Chew, Sparks, and Katkansky (1964).

Pinnotherid crabs of several species, best known as parasites of oysters, also occur in mussels. McDermott (1962) found that *Pinnotheres ostreum* and *P. maculatus* cause gill damage and palp erosion in *M. edulis*. Earlier, Atkins (1931b) described similar palp abnormalities in mussels from England.

CLAMS

Many species of bivalves called by the general term "clam" are harvested throughout the world. Some species constitute a significant commercial crop in many coastal areas; other species are fished for sport or are ignored. Changes in clam abundance have been documented, although mass mortalities comparable to those in oysters and mussels have not been reported. Mass deaths may pass unnoticed in sediment-hidden clams; it may be for this reason that information on diseases of clams is scarce. Among the diseases and parasites that are known in clams are: several protistan organisms, larval trematodes, larval cestodes, parasitic copepods, and tumors.

Microbial Diseases

Coe's (1955) study of population fluctuations of the California bean clam, *Donax gouldi* Dall, included a description of a possible fungus parasite "apparently similar to *Dermocystidium marinum*" as a cause of mass mortalities during the summer. Moribund clams of all ages were heavily infected with "irregularly spherical or ovoid cells, 2 to 6 microns in diameter." The identity of the pathogen was not further determined, however, and the information presented is insufficient to identify it as a *Dermocystidium.*

Much earlier, Léger (1897) found a coccidian, *Hyaloklossia pelseneeri,* in kidneys of *Donax* sp. and *Tellina* sp. in Europe, and Léger and Duboscq (1917) described another coccidian, *Pseudoklossia glomerata,* parasitic in *Tapes floridus* L. and *T. virgineus* L. from the Mediterranean Sea.

Ciliate parasites have been described from soft-shell clams, *Mya arenaria* L., by Uzmann and Stickney (1954). The peritrich *Trichodina myicola* Uzmann and Stickney was found, often in large numbers, on the palps. These infections were often accompanied by the nonpathogenic thigmotrich *Ancistrocoma myae* (Kofoid and Busch). *A. myae* had been described earlier from *M. arenaria* sampled in California (Kofoid and Busch, 1936; Kozloff, 1946) and in Massachusetts (Chatton and Lwoff, 1950). Kozloff considered the ciliate identical to *A. pelseneeri,* a common parasite of sea mussels. Fenchel (1965) also found *Ancistrocoma myae* in nearly 100 percent of *M. arenaria* sampled from two locations in Denmark.

Diseases Caused by Helminths

Several life history stages of diverse trematodes occur in the soft-shell clam. Uzmann (1952) reported sporocysts and cercariae *(Cercaria myae)* from gonads and digestive gland of this clam from Massachusetts, and held that parasitization resulted in a condition known as "water belly." (Subsequent observations, summarized by Dow and Wallace (1961), suggest that this condition may be a general sign of physiological disturbance.) Uzmann considered *C. myae* to be the same species as that reported by Stafford (1912) from the soft-shell clam in the Gulf of Saint Lawrence. Hutton (1953) believed that the larvae were members of the genus *Gymnophallus.* Stunkard and Uzmann (1958) discussed gymnophallid sporocysts and cercariae from the soft-shell clam, and Stunkard (1960) found echinostome metacercariae of the genus *Himasthla* in palps and gills of clams from the Maine coast. Three species were recognized. Earlier, Stunkard (1938) had demonstrated experimentally that cercariae of *Himasthla* would penetrate and encyst in the gills of *Mya arenaria* and a number of other bivalves, and Uzmann (1951) had reported natural occurrence of *Himasthla quissetensis* (Miller and Northrup) in *M. arenaria.* Susceptibility and response of a number of marine pelecypods, including four species of clams, to cercariae of *H. quissetensis* was tested experimentally by Cheng, Shuster, and Anderson (1966). Metacercariae were found in all clams and mussels but not in oysters used in the study.

Several larval trematodes have been reported from clams of the genus *Donax.* Giard (1897, 1907) identified bucephalid and gymnophallid cercariae. Rees (1939) found gymnophallid metacercariae, and Young (1953) described the life cycle of a monorchid, *Postmonorchis donacis,* whose larvae occur in the California bean clam. Hopkins (1958) identified sporocysts and cercariae of three species, and metacercariae of two species, in coquina clams, *Donax variabilis* Say, from the Texas coast. Infections by larval trematodes were considered by Pelseneer (1896, 1906, 1928) to be responsible for reduced abundance of *Donax vittatus* in France, and Coe (1946) held that trematode parasites (probably *Postmonorchis donacis*) were important in controlling population size in California *Donax gouldi.*

Fujita (1906, 1907, 1943) has described two larval trematode parasites of asari clams, *Tapes philippinarum* Adams and Reeve, from Japan. Parasitic castration of the hosts was observed.

Hopkins' (1957a) brief but excellent exposition of the role of parasitism in marine communities referred to an interesting interrelationship of host, parasite, and hyperparasite in the case of *Donax trunculus* parasitized by trematodes, which in turn were parasitized by the haplosporidan *Urosporidium pelseneeri* (Caullery and Chappellier). The often severe fluctuations in abundance of this clam have been attributed to shifts of balance in this tripartite relationship (Caullery and Chappellier, 1906; Cépède, 1911). Other haplosporidan and microsporidan hyperparasites of *Donax* have also been described (Guyénot, Naville, and Ponse, 1925; Dollfus, 1946; Mackin and Loesch, 1955).

MacGinitie and MacGinitie (1949) surveyed a number of species of clams from the Pacific coast of the United States for parasitization by larval tapeworms. Encysted larvae of the cestode genus *Anabothrium* were found, occasionally in large numbers, in the foot muscles of the gaper clam, *Schizothaerus nuttallii* Conrad. The definitive host of the *Anabothrium* sp. found in clams was identified by MacGinitie and MacGinitie as the bat stingray, *Myliobatis californicus.*

Sparks and Chew (1966) described remarkable levels of parasitization of littleneck clams, *Venerupis staminea* (Conrad), from Humboldt Bay, Calif., by larval tetraphyllidean cestodes of the genus *Echeneibothrium.* Cysts of the worm were closely packed throughout the tissues of the clams, which were abnormally exposed on the surface of gravel beds. Adult *Echeneibothrium,* with bothridia similar to those of larvae in clams, were found in bat stingrays caught in the same area.

Diseases Caused by Parasitic Crustaceans

Clams, like certain other bivalves, harbor parasitic copepods. Hoshina and Kuwabara (1959) described *Mytilicola mactrae* from Japanese *Mactra veneriformis* Reeve. About half the clams in a sample of 69 were infested. Yamaguti (1939) described another species from *Brachidontes senhausi* (Reeve), and Humes (1954) found *M. porrecta* in a single hard clam, *Mercenaria mercenaria* (L.), from the Gulf of Mexico.

Tumors

Hueper (1963) reported cauliflowerlike papillary tumors at the anterior end of soft-shell clams collected from Chesapeake Bay. He termed the condition "endemic" and reported it in about 2 percent of clams collected from certain bay areas.

OTHER BIVALVE MOLLUSKS OF COMMERCIAL IMPORTANCE

There are two other groups of commercially important bivalve mollusks—scallops and pearl oysters—for which some information on diseases and parasites is available. Mass mortalities caused by disease have not been reported in either group. Scallops are infected by protozoan and trematode parasites, and occasionally are affected by a shell disease. Pearl oysters harbor a number of larval trematode parasites.

Scallops

Although major mortalities have occurred in scallop populations (Dickie and Medcof, 1963; Medcof and Bourne, 1964; Merrill and Posgay, 1964; Sanders, 1966), none has been definitely associated with disease. In fact, only a few diseases and parasites are known, and their effects on the hosts are slight.

Two parasites of scallops have been recognized. A coccidian, *Pseudoklossia pectinis,* was described as a rare parasite in the kidney tubules of the great scallop, *Pecten maximus,* at Roscoff, France, by Léger and Duboscq (1915b), who found usually light infections with no extensive pathology. Sporocysts and fork-tailed cercariae of a trematode (not further identified) were found by Linton (1915) in large bay scallops, *Aequipecten irradians,* from Woods Hole, Mass. Infections were rare.

An abnormal brown discoloration of meats was studied by Medcof (1949) in sea scallops, *Placopecten magellanicus* (Gmelin), off the south coast of Nova Scotia, Canada. He considered the condition to result from extensive invasion of the shell by a boring sponge. In advanced stages, the shell was completely honeycombed, causing excessive inner shell deposition and producing weak shrunken individuals which, Medcof assumed, died eventually from effects of the shell disease. Meat yields from heavily infected scallops were less than half those of normal individuals, but only older scallops (8 or 9 years old) were infected.

Pearl Oysters

Pearl-producing bivalves of the family Pteriidae, called "pearl oysters" but actually taxonomically remote from edible oysters of the family Ostreidae, occur in many parts of the world (Sivalingam, 1962). Interest in parasites of pearl oysters has naturally centered on those larval worms considered responsible for pearl formation (Jameson, 1902, 1912; Wright, 1966), but a few other parasites and diseases have been recognized.

Parasites of the pearl oysters of Ceylon, *Margaritifera (Pinctada) vulgaris* Schum., were studied by Shipley and Hornell (1904) and Southwell (1911, 1912) particularly with regard to the role of parasitic worms in pearl formation. These authors described several stages of cestode larvae, some clearly trypanorhynchid, from the digestive gland and gills of the pearl oyster. The worms occurred, often in great numbers, in fibrous capsules. Several larval trematodes were also found, but only one, described as *Muttua margaritiferae,* occurred in abundance. Metacercariae localized in the gills. Other metacercariae, described as *Musalia herdmani,* were found in the muscles, mantle, and foot. An aspidobothrid trematode, *Aspidogaster margaritiferae,* occurred in the pericardial cavity, and several species of encysted larval nematodes were seen in the gonads, stomach walls, and adductor muscles.

Pearl oysters of Japan, *Pinctada martensii,* are commonly infested with sporocysts and cercariae of a bucephalid trematode described as *Bucephalus margaritae* by Ozaki and Ishibashi (1934). Experimental infections of several species of small fishes with cercariae from pearl oysters (Sakaguchi, 1962, 1966a) produced metacercariae morphologically the same as those identified as *B. varicus* by Manter (1940). Adult trematodes were found in the digestive tracts of carangid fishes, *Caranx sexfasciatus* and *C. ignobilis,* which were abundant in the waters near oyster farms where pearl oysters were heavily infested (Sakaguchi, 1966b). Marked decline in condition of pearl oysters resulted from invasion by larval trematodes. Sporocysts were found to overwinter in the host, and cercarial production began again when water temperatures rose in spring (Sakaguchi, 1965). Pearl oysters infected in the preceding year suffered high mortalities after insertion of pearl cores, and high percentages of pearls produced by infected individuals were of low quality (Sakaguchi, 1964).

DISEASES OF CRUSTACEA

Crustacea such as crabs, lobsters, and shrimps are among the most valuable of marine crops in many parts of the world. Large populations of crustaceans occur on the continental shelves, and often part or all of the life cycle is spent in estuarine or inshore waters. Here individuals may be observed and studied in natural habitats as well as in the landed catches. These studies have disclosed certain parasites and diseased conditions. Disease may have severe effects on survival, particularly when crabs and lobsters are impounded before sale. Diseases exist in natural populations of Crustacea as well, although effects are less apparent than in captives or in more sedentary marine animals. No widespread epizootic is known for marine Crustacea that would be comparable to "krebspest," a fungus disease that swept through populations of freshwater crayfishes of Europe (Schikora, 1906, 1926; Schäperclaus, 1935; Nybelin, 1935; Mannsfield, 1942).

CRABS

Many species of crabs have great commercial value in various parts of the world. Consequently, diseases and parasites have been included in studies of factors which affect abundance. Microbial diseases, helminths, and parasitic crustaceans occur in crabs.

Microbial Diseases

Among the microbial diseases of crabs are those caused by a virus, several fungi, bacteria, and a variety of protozoans.

Viruses.—Virus diseases have not been reported from marine invertebrates, with the exception of one described recently, and only very briefly, by Vago (1966), in swimming crabs, *Portunus depurator* (L.), from the French Mediterranean coast. Gross disease signs included the slow development of paralysis, and sometimes a slight darkening (presumably of the exoskeleton) in later phases of the disease. Virus particles were seen with the electron microscope; inoculation of blood from infected animals produced disease signs in healthy crabs; and infections were obtained with ultrafiltrates and ultracentrifugates of homogenized tissues from sick crabs. No indication of disease prevalence was given by Vago.

Recently, Sprague and Beckett (1966) have published a preliminary note on a disease of soft-shell and molting blue crabs, *Callinectes sapidus* Rathbun. The disease, of undetermined but possibly viral etiology, was called "gray crab disease." It occurred in crabs from seaside bays of Virginia, where it apparently caused some deaths among captive crabs.

Bacteria.—King crabs, *Paralithodes camtschatica* (Tilesius) and *P. platypus* Brandt, from the eastern North Pacific are occasionally affected by "rust disease," which seems to result from action of chitin-destroying bacteria on the exoskeleton. Microorganisms of this type are common in the sea (ZoBell and Rittenberg, 1938; Hock, 1940, 1941) but usually degrade the exoskeletons of dead animals and do not affect living individuals. Over thirty species of chitin-destroying bacteria are known, of which half have been isolated from shells of crustaceans.

Bright, Durham, and Knudsen[3] described observations of rust disease in landed catches of king crabs from Kachemak Bay, Cook Inlet, Alaska, as well as experimental studies of the bacteria involved. The disease was characterized by progressive darkening and softening of the exoskeleton, particularly on the ventral surfaces. Underlying living tissues were unaffected. Natural infections reached 11 percent in larger older crabs in 1957 but were much lower in 1958 and 1959. Shell abrasions and injuries served as foci of the disease, which developed experimentally within 2 weeks. The disease was not carried over to the new exoskeleton after molting, but recently shed crabs were highly susceptible because the new shell was easily punctured or abraded. Chitin-destroying bacteria were isolated from infected crabs, and cultured organisms produced the disease experimentally in normal crabs. Similar bacteria were also isolated from sea water in Kachemak Bay. The authors concluded that the disease would not affect the commercial fishery seriously unless the catch of crabs was substantially less than annual recruitment, since larger individuals, which do not molt annually, were more frequently infected.

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[3] Data furnished from unpublished contract report, "King crab investigations of Cook Inlet, Alaska," by Donald B. Bright, Floyd E. Durham, and Jens W. Knudsen of the Allan Hancock Foundation, University of Southern California, Los Angeles, to BCF Biological Laboratory, Auke Bay, Alaska, June 1960. (Cited with permission of Laboratory Director, BCF Biological Laboratory, Auke Bay, Alaska.)

Fungi.—Eggs of blue crabs from lower Chesapeake Bay were found to be parasitized by a fungus *Lagenidium callinectes* Couch (Couch, 1942; Sandoz, Rogers, and Newcombe, 1944; Sandoz and Rogers, 1944; Newcombe and Rogers, 1947; Rogers-Talbert, 1948). Infected eggs either failed to hatch, or gave rise to abnormal zoea larvae. Infection levels were as high as 90 percent of a sample of ovigerous female crabs, and up to 25 percent of the eggs in a "sponge" (egg mass). Penetration of the egg mass was slow and did not exceed 3 mm. This fact, combined with the short (2-week) incubation time, permitted normal development of much of the egg mass internal to the infection. Experimentally, the fungus developed normally in salinities from 5 to 30 o/oo. The fungus was transmitted experimentally to the eggs of two other species of crabs (the oyster crab and the mud crab, *Neopanope texiana* Rathbun) inhabiting the same Bay area.

Pea crabs *(Pinnotheres)* taken from the sea mussel at Plymouth, England, were parasitized by the fungus *Leptolegnia marina* (Atkins, 1929, 1954a). The mycelium was usually found in the gills but penetrated other body organs and appendages as well. Zoosporangia developed in the appendages, and large numbers of zoospores were released upon the death of the host. No further growth of the fungus took place in dead crabs, and no external development, beyond papillae of zoospore exit tubes, was seen. Atkins (1954b, 1955) described two other fungi, *Plectospira dubia* and *Pythium thalassium,* which infect eggs of pea crabs and other Crustacea.

Protozoa.—Gregarines are common parasites of many Crustacea, and an extensive and at times confusing literature has accumulated. Many members of the group have been reported from crabs. For example, species of the genus *Cephaloidophora* occur in spider and fiddler crabs of the United States east coast (Watson, 1915, 1916a, 1916b; Kamm, 1922), in the striped shore crab, *Pachygrapsus crassipes,* of the Pacific coast, and in the Mediterranean "flat crab," *Pachygrapsus marmoratus* (Ball, 1938; Théodoridès, 1961, 1962). As mentioned in the discussion of oyster diseases, several representatives of the genus *Nematopsis* occur in Atlantic species of mud crabs (Prytherch, 1940; Ball, 1951; Sprague and Orr, 1955). Although the gregarines are not usually considered serious pathogens of Crustacea, Ball pointed out that masses of the parasites may occlude the lumen of the intestinal caeca and may cause sloughing or thinning of the epithelium.

Several microsporidans are parasites of crabs. Sprague (1965a) described a species of *Nosema* parasitic in muscles of the blue crab. Infected muscles became opaque with a coarse fibrous texture, and heavy infections caused lysis of myofibrils. He considered the parasite to be common and widespread in Chesapeake Bay, and believed it might be a significant factor in crab mortality. Sprague (1966b) also described *Plistophora cargoi* from the skeletal and cardiac muscles of a single blue crab from the Patuxent River, Md. Earlier, Perez (1905a, 1905b) reported *Nosema pulvis* in the muscles of the green crab, *Carcinus maenas* (L.), and Perez (1907) also described ovarian infections with a microsporidan, *Thelohania maenadis,* in green crabs from Arcachon, France. The parasite normally occurred in the body muscles.

Ciliates are also significant parasites of crabs. Serious mortalities of molting blue crabs from Chesapeake Bay occurred in the summers of 1965 and 1966. Their gills had a massive infestation of peritrichous ciliates (fig. 7) of the genera *Lagenophrys* and *Epistylus* (Couch, 1966, 1967a). Mortalities were most severe among crabs in holding tanks just before or after molting, but wild crabs were also heavily infested, and fishermen reported mortalities. Infestations of gills frequently seemed heavy enough to interfere with respiration.

Another ciliate, *Anophrys sarcophaga* Cohn, is found in the blood of green crabs. Originally described as a free-living form (Cohn, 1866), it was first seen in the blood of crabs by Cattaneo (1888). Poisson (1930) described the

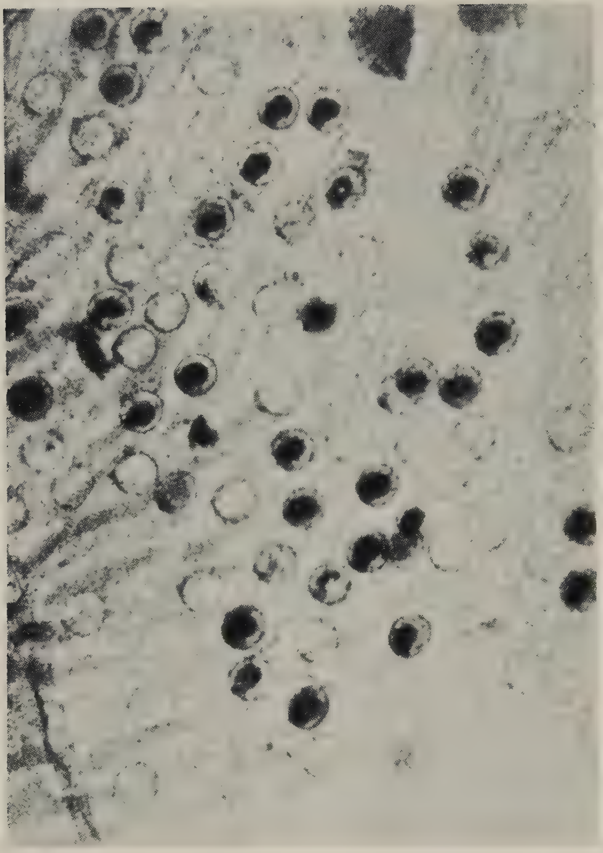

FIGURE 7.—*Lagenophrys* encysted on gills of blue crab (× 70).

active and encysted forms of the parasite in great detail. He also cultured the organism. *Anophrys* apparently ingests large numbers of host amebocytes, and multiplies until the blood becomes a dense "soup" of motile parasites. The disease, though often fatal once infection occurred, was relatively rare on the French coast. Experimental infections, achieved by injecting the ciliates, killed crabs in 2 to 7 days. Certain individual crabs seemed resistant to infection, but no antibody response was detected. Effects on the parasites included inhibition of reproduction, immobilization, and eventual death.

Diseases Caused by Helminths

Helminth infestations include larval trematodes and cestodes, as well as nemerteans and leeches.

Trematode metacercariae are common in several species of crabs. Larvae of *Microphallus* (*Spelotrema*) *nicolli,* encysted in body muscles of blue crabs, were described by Cable and Hunninen (1940). Adult trematodes occur in young herring gulls, *Larus argentatus,* and sporocyst generations in the snail *Bittium alternatum* (Say). A haplosporidan hyperparasite, *Urosporidium crescens* [De Turk], has been found in metacercariae of *Microphallus nicolli* from blue crabs caught in North Carolina (Anonymous, 1940). One third of the crabs examined contained metacercariae, but the extent of hyperparasitization was not determined. The host metacercarial tissue was often completely destroyed, leaving little more than a sack of protozoan spores. Invasion by *Urosporidium* was thought to occur before encystment of cercariae. Masses of dark pigmented spores in the destroyed metacercaria produce a black spot, which has led to the application of the descriptive colloquial term "pepper crab" to hyperparasitized individuals. "Pepper spots" occur most commonly in fat bodies, digestive gland, and muscles of the crab.

Metacercariae of *Microphallus* (*Spelotrema*) *carcini* Lebour were reported from the hepatopancreas of green crabs from the English Channel (Guyénot et al. 1925), the Mediterranean (Timon-David, 1949), and elsewhere. Hyperparasitization of metacercariae by the microsporidan *Nosema (Plistophora) spelotremae* was reported by Guyénot et al. Metacercariae of *Microphallus similis* (Jägerskiöld) occur in the hepatopancreas of the green crab of the western North Atlantic (Stunkard, 1957). Young green crabs were killed in 10 to 20 days by massive experimental exposure to cercariae of *M. similis.*

Larval diphyllidean cestodes (*Echinobothrium affine* Diesing) have been reported by Dollfus (1964a, 1964b) from green crabs sampled at Roscoff on the coast of France.

Juvenile nemerteans, *Carcinonemertes carcinophila* (Kölliker), encyst on the gills of the blue crab. After the female crab spawns, the worms excyst and migrate to the egg mass, where they mature, lay eggs, then return to the gills (Davis, 1965). Hargis (1959) has cited this parasite as an indicator of host physiology, since Hopkins (1947) pointed out that increased size and more noticeable color were characteristic of reencysted worms after the host has spawned. This and other nemerteans have been described from a number of crabs, including the green crab, of Europe (Coe, 1902; Humes, 1942).

A localized mortality of blue crabs, thought to be caused by parasitization by leeches, *Myzobdella lugubris* Leidy, was reported from a Florida river by Hutton and Sogandares-Bernal (1959). A sample of 7 crabs had 32 leeches attached near the base of the legs and near perforations in the exoskeleton. The parasite is known from the Atlantic and Gulf coasts of the United States but had not previously been considered to cause mortalities (Moore, 1946).

Other leeches occur on crabs. Oka (1927) described *Carcinobdella kanibir* from Japanese edible crabs, *Chionoecetes opilio*. Egg cases and adults of the leech *Notostomobdella cyclostoma* (Johansson) are common on Alaska king crabs, particularly during summer (Moore and Meyer, 1951; Bright et al., see footnote 3). Undescribed worms, probably leeches, were seen by MacKay (1942) on the abdomens of female Dungeness crabs, *Cancer magister* Dana, from British Columbia. The worms were much larger on egg-bearing crabs and were found chiefly among the eggs.

Diseases Caused by Parasitic Crustaceans

Parasitic crustaceans—rhizocephalans, isopods, and copepods—also infest crabs.

Many species of crabs, in many parts of the world, are parasitized by rhizocephalan Cirripedia. These parasites invade the host's body and cause degeneration of the gonads (Reinhard, 1956). The tumorlike body of the rhizocephalan ramifies throughout much of the crab and causes extensive morphological changes. The crab is usually sterilized, secondary sex characters are modified, and molting is often inhibited (Giard, 1888; Potts, 1906; Smith, 1906; Cantacuzène, 1925; Reinhard, 1950; Ichikawa and Yanagunachi, 1957).

Brachyuran or true crabs are parasitized by members of the rhizocephalan family Sacculinidae. In U.S. waters, crabs most frequently parasitized are the green crab of the Atlantic coast, and the masking crab, *Loxorhynchus grandis*, the kelp crab, *Pugettia producta* (Randall), and the black-clawed crab, *Lophopanoepeus bellus* (Stimpson) of the Pacific coast. Green crabs and swimming crabs, *Macropipus* (*Portunus*) *holsatus* (Fabricius), from the English coast are parasitized by *Sacculina carcini* Thompson (Delage, 1884; Day, 1935; Foxon, 1940). Blue crabs from the Gulf of Mexico are parasitized by the rhizocephalan *Loxothylacus texanus* (Hopkins, 1957a). Mud crabs, *Eurypanopeus depressus* (Smith), from lower Chesapeake Bay (Virginia) were discovered by Van Engel, Dillon, Zwerner, and Eldridge (1966) to have high incidences of the sacculinid *Loxothylacus panopaei* (Gissler). The localized nature of the infestations suggested that the parasite had been introduced with its hosts in shipments of oysters from the Gulf of Mexico.

Many species of anomuran crabs may be parasitized by rhizocephalans. King crabs, *Paralithodes platypus*, from Alaskan waters are occasionally invaded, probably by a species of *Peltogaster* (J. B. Kirkwood, written communication, April 14, 1967). Hermit crabs are also frequently invaded by members of the family Peltogastridae. Reinhard (1942), who examined 3,092 *Pagurus pubescens* Krøyer from the Maine coast of the United States, found 13.7 percent parasitized by *Peltogaster paguri* Rathke. The same rhizocephalan occurs on the coast of France, where its host is *Pagurus bernhardus* (L.) (Perez, 1927, 1928, 1931a, 1931b, 1931c). Infestation can have significant effects on crab populations, since parasitization usually causes degeneration of host gonads. Perez (1929, 1931a), however, found interesting evidence for sterilization and mortalities of *Peltogaster paguri* because of hyperparasitization by the epicaridean isopod *Liriopsis pygmaea* (Rathke); in some samples from northern France, most of the rhizocephalans were parasitized. Perez believed that this parasitization was an important control for *Peltogaster* populations.

Epicaridean isopods can also be significant parasites of crabs. Two families are of importance: the Bopyridae, which live principally in the gill chambers, and the Entoniscidae, which invade the haemocoele. In some species morphological modification for parasitic existence parallels that in rhizocephalans (Veillet, 1945). Effects on the crab host often include sterilization and changes in secondary sexual characteristics (Tucker, 1930; Reverberi, 1943, 1952;

Reinhard and Buckeridge, 1950). Parasitization of crabs by female entoniscids causes internal deformities, including reduction in size of organs (Atkins, 1933; Reinhard, 1945) and changes in the nervous system (Matsumoto, 1953).

Copepods are known as parasites of crab eggs. Connolly (1929) described *Choniosphaera cancrorum* from the egg masses of the American rock crabs, *Cancer borealis* and *C. irroratus.* Johnson (1957) found the same species on green crabs from the Maine coast. Gnanamuthu (1954) described *Choniosphaera indica* from gills and egg masses of an Indian edible crab, *Neptunus sanguinolentus.* Copepod larvae were found between the crab's gill lamellae, probably feeding on tissue fluids; adults apparently suck fluids from the crab eggs. Many other species of copepods, particularly of the family Choniostomatidae, are parasitic on Crustacea (Hansen, 1897, 1904, 1923).

An extensive and fascinating body of literature on rhizocephalan, epicaridean, and other crustacean parasites and hyperparasites of Crustacea has accumulated (Giard and Bonnier, 1887, 1895; Smith, 1906; Shiino, 1942; Veillet, 1945; Reinhard, 1944, 1956; Baer, 1951; Nicol, 1960).

LOBSTERS

Lobsters, because of their great economic importance in North America and Europe, have been subjects of many scientific studies, including some concerned with diseases and parasites. Because of the practice of holding lobsters in pounds and live cars, occasionally for extended periods and frequently under crowded conditions, mortalities have been observed and causes examined. Two bacterial diseases have significant effects on impounded lobsters. Among the known larger parasites are trematodes, nematodes, acanthocephalans, and annelid worms.

Microbial Diseases

A bacterial disease, caused by gram-positive tetrad-forming encapsulated cocci, described as *Gaffkya homari* Hitchner and Snieszko, is known from wild and impounded populations of American lobsters, *Homarus americanus* Milne-Edwards. The disease (gaffkaemia) was first noted on the Maine coast in 1946 (Hitchner and Snieszko, 1947; Snieszko and Taylor, 1947; Getchell, 1949). "Red-tail" disease, as it was originally called, is characterized by a variable pink coloration of the ventral abdomen, pink blood, prolonged clotting time, and drastic reduction in blood phagocytes. Infected lobsters become progressively weaker, and mortalities may reach 50 percent after short periods of storage. Mortalities increase sharply if water temperature exceeds 15° C. Moribund lobsters move to shoal water and die in a "spread-eagle" position.

Goggins and Hurst (1960)[4] have provided information about two epizootics of gaffkaemia along the entire Maine coast, one in 1946–47 and another in 1959–60, with losses as great as 58 percent of impounded populations. They found that the pathogen could live and multiply outside the lobster, in the slime on lobster cars, crates, tanks, and live wells. *Gaffkya* was also isolated from mud of tidal pounds and from sea water several miles from infected pounds. The disease was transmitted directly by allowing presumably healthy lobsters to feed on infected individuals or by holding healthy lobsters in sea water containing the pathogen. Incubation time was 14 to 21 days, although the animals possibly were already gaffkaemic before the start of the experiments. Treatment of tidal pounds with calcium hypochlorite reduced populations of the pathogen in bottom mud and reduced subsequent losses of impounded lobsters.

The disease organism is often present in wild populations. Stewart and MacDonald (1962) and Stewart, Cornick, Spears, and McLeese (1966) isolated *Gaffkya* from 96 of 2,035 recently caught lobsters in Canada and found the disease to be widespread in the Canadian Atlantic region. Cornick and Stewart (1966) recovered, from presumptive tests for *Gaffkya* in Canadian lobsters, several other kinds of bacteria, including *Micrococcus, Pseudomonas, Achromobacter,* and *Brevibacterium*—none of which was considered to be pathogenic. Rabin (1965) found a *Gaffkya*-like organism in lobsters from Woods Hole, Mass., and Wood (1965a, 1965b) isolated *Gaffkya*-like organisms from two European lobsters (*Homarus vulgaris* Milne-Edwards) from the North Sea. Wood observed lobster mortalities in storage tanks in southern England in 1962 and recovered *Gaffkya* with cultural and biochemical characteristics similar to Canadian and United States isolates. Epizootics of gaffkaemia have been reported from European lobsters in Ireland (Gibson, 1961), Norway, and the Netherlands (Roskam, 1957). Gibson noted that diseased lobsters were also infested with the "gill maggot," *Nicothoë astaci* Audouin and Milne-Edwards, which was absent from uninfected individuals. Cross sections of the parasitic copepod were used by Gibson to determine the presence of the disease in the host.

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[4] Data provided in unpublished mimeographed report of Department of Sea and Shore Fisheries, Augusta, Maine, "Progress report on lobster gaffkyaremia (Red Tail)," by P. L. Goggins and J. W. Hurst, 1960.

Experimental studies of host-parasite relationships showed that lobsters became infected and died a few days after inoculation with *G. homari* (Rabin, 1965). Prior inoculation with *Vibrio* endotoxin did not enhance the infection and prior inoculation of heat-killed *Gaffkya* did not alter the course of infection. Lobster serum stimulated in vitro growth of *G. homari* in almost every test, but growth of *Vibrio* was sometimes inhibited. Studies of possible defense mechanisms of lobsters against *G. homari* have also been carried out at the Halifax (Nova Scotia) and Saint Andrews (New Brunswick) stations of the Fisheries Research Board of Canada (Fisheries Research Board of Canada, 1966). Lobster serum, as indicated by Rabin's work, had no bactericidal activity against the pathogen but instead promoted its growth.

A preliminary note by Bell and Hoskins (1966) described experimental transmission of *G. homari* to Dungeness crabs and spot shrimps (*Pandalus platyceros*). Infection was achieved by intramuscular inoculation, but not by ingestion or contact. Mortalities were produced in both species.

A second bacterial disease of lobsters, known as "shell disease" (Hess, 1937), is caused by chitin-destroying gram-negative bacilli. Hess isolated chitin-degrading bacteria from live lobsters impounded at Yarmouth, Nova Scotia, but collected from various parts of the Canadian Maritime provinces. This was the first report of attacks by such microorganisms on living Crustacea. The disease was characterized by a pitting and sculpturing of the exoskeleton (fig. 8); although it was first seen in impounded lobsters, similar conditions were later observed in freshly caught lobsters from several widely separated Canadian fishing grounds. Initial lesions occurred on the walking legs, and were distinguished by white outer margins, from which the bacteria were most readily isolated. Hess found the disease relatively rare in natural populations but noted severe shell erosion and weakening of lobsters stored in pounds over the winter. Microorganisms isolated were biochemically and physiologically similar to *Bacillus chitinovorous* Type II and Type XIV of Benton (1935). All isolates were able to decompose pure chitin in saline solution containing no other nitrogen or carbon source. None of Hess' isolates—nor, for that matter, isolates

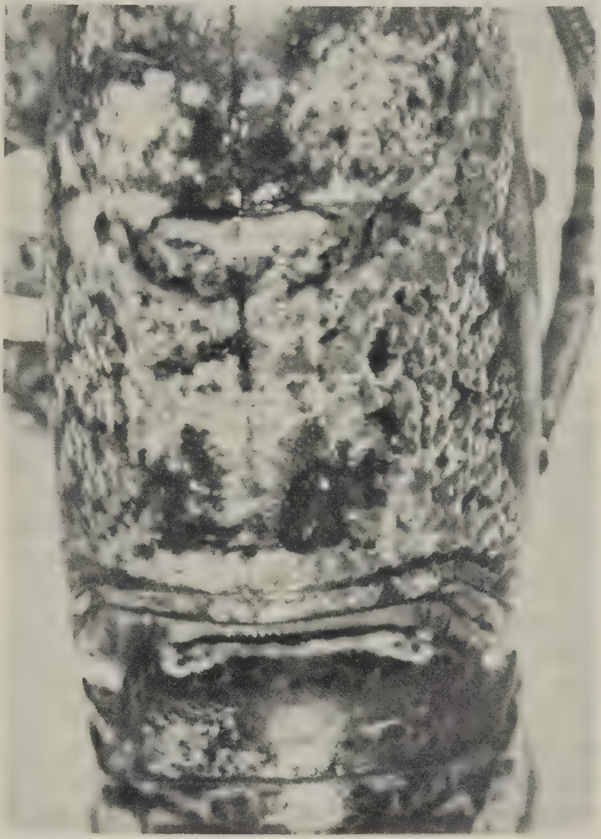

FIGURE 8.—"Shell disease" of American lobster.

prepared in subsequent work—was reported to reproduce the disease experimentally.

Significant mortalities of lobsters accompanied the shell disease; Taylor (1948) found that 71 percent of infected captive lobsters died from the disease, but observed no correlation between mortality and intensity of external shell erosion. Contraction of the disease by healthy lobsters placed in sea-water tanks with infected individuals indicated direct transmission. The disease developed slowly, requiring at least 3 months before the advanced stages were reached. Progress of chitin destruction was directly temperature-dependent, and new shell laid down after molting was not affected, except by reinfection.

Sawyer and Taylor (1949) observed that shell disease produced thickening or complete destruction of the chitinous layer of the gill filaments. No living gill tissue was attacked, but the authors postulated respiratory impairment as an important consequence of the disease. The infection appeared to be entirely external, confined to the exoskeleton, and not invading living tissue nor transmitted internally. Sawyer and Taylor also reported the disease to be present on the Maine coast as well as in Canada, and considered it a potential threat to the lobster industry, in view of the ease of transmission and the observed mortalities of captive individuals. The method of infection of lobsters is unknown; lodging of bacteria in pores and ducts of the shell was proposed by Sawyer and Taylor as a route of invasion.

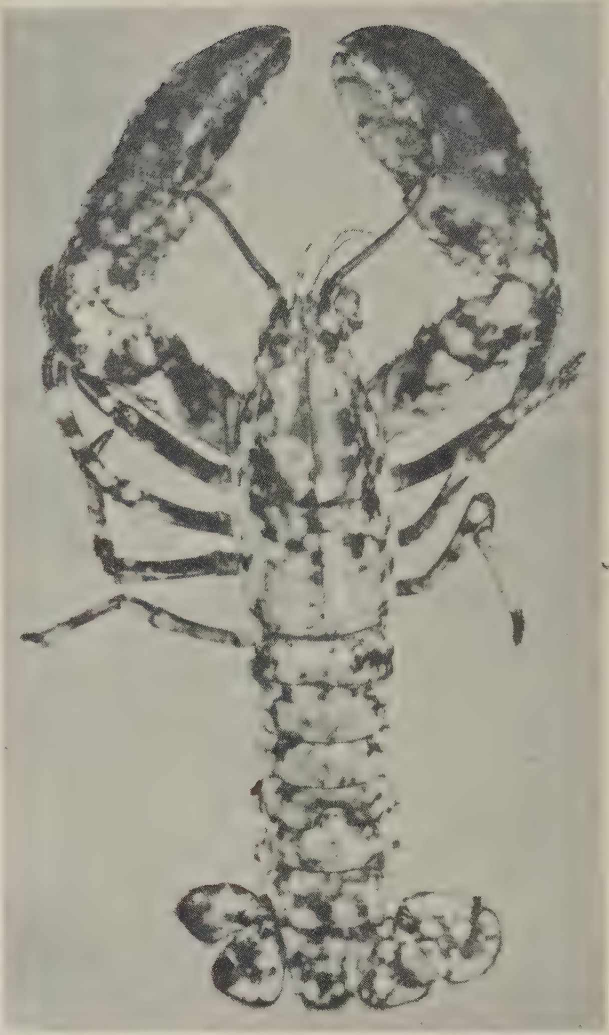

FIGURE 9.—"Leopard lobster" with external signs of mottling disease.

Another recently recognized disease of lobsters from the Maine coast, probably of fungus etiology, is called "mottling disease." Characterized by yellowish splotches in an otherwise dark green exoskeleton (fig. 9), the condition has been known for many years as a color variation. Affected individuals are called "leopard lobsters" (Herrick, 1895, 1911). The shell condition and color result from progressive growth of areas of necrosis in underlying tissues and, in advanced cases, even blisters of the shell. The areas of necrosis expand slowly in lobsters held in sea water tanks. Our histological examination of diseased tissues disclosed numerous Schiff-positive, subspherical, heavy-walled bodies 30 to 60μ in diameter. Tentatively, the organism is considered a chytrid fungus. Preliminary attempts at culture and transmission have been unsuccessful. The disease occurs infrequently in Gulf of Maine lobster populations and has not been reported from other areas.

Dannevig (1928, 1939) in a report on Norwegian lobster hatcheries, described infection and destruction of eggs on the female by the suctorian *Ephelota gemmipara* Hertwig. The protozoan was found on newly caught individuals, and increased tremendously on lobsters in hatching boxes. Dannevig attributed substantial decreases (90 percent) in production of larvae to the effects of the parasite. The organism was abundant only in certain years.

The gregarine protozoan, *Porospora gigantea* (Van Beneden), has been reported as parasitic in the digestive tract of the European lobster (Hatt, 1928, 1931), and was found in all of 202 American lobsters examined from the Magdalen Islands, Gulf of Saint Lawrence, Canada, by Montreuil (1954). *Porospora nephropis* has been described from the Norway lobster, *Nephrops norvegicus* L., by Léger and Duboscq (1915a) and Tuzet and Ormières (1962).

"Spiny lobsters" (family Palinuridae) are of economic importance in many parts of the world, but little is known about their diseases (Sims, 1966). One fatal and apparently infectious disease of *Panulirus argus* (Latreille) from Florida waters was observed by H. W. Sims (written communication, April 8, 1967). Affected individuals became disoriented and their abdomens were "milky"—a condition reminiscent of microsporidan infections of shrimps (Sprague, 1950a) and fresh-water crayfishes (Sprague, 1950b; Sogandares-Bernal, 1962), as was pointed out by Sims. Two fungus parasites, *Ramularia branchialis* and *Didymaria palinuri,* have been described recently from the gills of *Panulirus vulgaris* in Italy by Sordi (1958). *R. branchialis* was also found on the gills of *Homarus vulgaris.*

Diseases Caused by Helminths

Immature aspidobothrid trematodes, *Stichocotyle nephropis* Cunningham, encyst in the stomach and intestinal walls of lobsters—*N. norvegicus* and *H. americanus*—from Europe and North America (Cunningham, 1887; Nickerson, 1894; Herrick, 1895; Odhner, 1910; Montreuil, 1954; MacKenzie, 1963). Montreuil found the parasite in lobsters taken near the mouth of the Bay of Fundy in the Gulf of Maine but not in more than 500 lobsters examined from the Gulf of Saint Lawrence. Adult *S. nephropis* parasitize several species of skates and rays (Odhner, 1898; Linton, 1940).

A larval nematode, tentatively assigned to the genus *Ascarophis* Van Beneden, has been recognized from lobsters taken off northeastern United States (Anonymous [Uzmann], 1966; Uzmann, 1967a). Adults of the genus occur in fishes, particularly gadoids (Uspenskaya, 1953). Larvae occurred commonly in lobsters from Georges Bank and several canyons along the edge of the Continental Shelf south of Cape Cod, Mass., but were absent in lobsters from near the coast. The larvae were encysted in the rectal wall of 25 percent of the offshore lobsters examined by Uzmann, who speculated that larvae from lobsters reach maturity in abundant cod (*Gadus morhua* L.) and haddock (*Melanogrammus aeglefinus* (L.)) populations of Georges Bank.

A larval acanthocephalan, probably of the genus *Corynosoma,* was identified in American lobsters from the Gulf of Saint Lawrence and elsewhere in the Canadian Maritime Provinces by Montreuil (1954). The worms were usually encysted in the thin wall of the intestine, although some had apparently perforated the gut and encysted in the heart and body muscles. Montreuil believed that accidental gut perforation may provide a route of entry for secondary invaders, and account for appreciable mortality. Feeding experiments with cats and seals suggested that the stage of *Corynosoma* in the lobster is not infective to mammals.

Havinga (1921), in a discussion of artificial lobster rearing in the Netherlands, described the attachment of a small green annelid worm, *Histriobdella homari* Van Beneden, to the eggs and to all parts of the bodies of larval and adult lobsters in Norway. He attributed poor success in production of larvae to effects of the worm. The same parasite had been observed earlier (Sund, 1914, 1915) in massive numbers on eggs of lobsters held in floating boxes at Korshavn, Norway, where it was held responsible for destruction of the brood. Every female lobster was infested with thousands of worms, and they also occurred on larvae. Although *H. homari* had not been reported previously from American lobsters, Uzmann (1967b) has recently found it to be widely distributed on the gills of lobsters in New England coastal waters from Maine to Connecticut, and on those from Georges Bank as well.

Diseases Caused by Parasitic Crustaceans

A blood-sucking parasitic copepod, *Nicothoë astaci* Audouin and Milne-Edwards, has been found on the gills of European lobsters. The parasite was prevalent in Scottish waters (Thomas, 1954; Mason, 1958, 1959) and was seen by Korringa (1957b) in lobsters being held in the Netherlands. Mason found infestations to be occasionally heavy, with a maximum of 1,700 copepods on a single lobster. He concluded that such heavy infestations could harm the host through loss of blood and reduction in gill surface available for gas exchange, but that the usual level of infestation (100 or less per lobster) caused little or no harm to the host

Tumors

One of the earliest observations of neoplasms in invertebrates, according to Scharrer and Lochhead (1950), was made by McIntosh and reported by Prince (1897). A lobster tumor originated in the stomach wall and pushed through the carapace behind the eyes, enlarged, and finally killed the lobster.

SHRIMPS

Many shrimps of the families Penaeidae and Pandalidae are of worldwide commercial significance. Shrimps are the most valuable fishery resource in the United States (Lyles, 1966). Parasites and diseases, which may have adverse effects on shrimp stocks, have been studied, particularly in the Gulf of Mexico. Several diseases caused by Microsporida are known, and larval helminths—trematodes, cestodes, and nematodes—have been reported. Isopods and rhizocephalans have also been observed.

Microbial Diseases

Protozoan parasites have been shown to be of significance to commercial shrimp populations of the Gulf of Mexico. Several microsporidan Protozoa cause a condition known as "cottony" or milky" shrimps. *Nosema nelsoni* was described by Sprague (1950a) from the brown shrimp, *Penaeus aztecus* Ives. Affected body muscles had an opaque white discoloration, and black pigment spots occurred externally. The disease was common in bait shrimps as well as in those processed as food. Infected individuals did not survive well in bait tanks and were also discarded in processing plants, thus representing significant losses to the industry (Woodburn, Eldred, Clark, Hutton, and Ingle, 1957; Hutton, Sogandares-Bernal, and Eldred, 1959). Sprague (1950a) found microsporidan spores in the gonads of the white shrimp, *P. setiferus* (L.), some of which he described as *Thelohania penaei*. Earlier, Viosca (1945) reported that "about 90 percent" of white shrimp in Louisiana waters were infected in 1919 by a protozoan disease (not further identified) which destroyed the reproductive organs. If the disease was caused by *T. penaei*, the microsporidan may play a role in fluctuations of the host species when present at epizootic levels. Iversen and Manning (1959) described still another microsporidan, *Thelohania duorara*, from the musculature of pink shrimp, *P. duorarum* Burkenroad, of the Gulf of Mexico. Infected individuals were relatively rare, however, in landed catches. Brazilian brown shrimp, *P. brasiliensis*, also harbor the same parasite (Iversen and Van Meter, 1964).

Several gregarine Protozoa also occur in shrimps. Sprague (1954) tentatively identified as *Nematopsis penaeus* a gregarine from the digestive tract of brown shrimp from Louisiana. The same parasite was observed by Kruse (1959a, 1959b) and Hutton, Sogandares-Bernal, Eldred, Ingle, and Woodburn (1959) in several species of shrimps from Florida. Sprague mentioned the possibility of extensive damage to the intestinal epithelium of individuals heavily infected by *Nematopsis*. Kruse described a second gregarine from the digestive tracts of brown and pink shrimps in Florida, and Hutton, Sogandares-Bernal, Eldred, Ingle, and Woodburn (1959) observed the same parasite with high frequency in certain samples of pink shrimp from Florida.

Diseases Caused by Helminths

Shrimps occasionally harbor larval helminths. Metacercariae of the trematode *Opecoeloides fimbriatus* (Linton) were found by Hutton, Sogandares-Bernal, Eldred, Ingle, and Woodburn (1959) and Sogandares-Bernal and Hutton (1959) in several Florida species. Larval *Microphallus* sp. have been reported from the body muscles and hepatopancreas of pink shrimp (Hutton, Sogandares-Bernal, and Eldred, 1959; Hutton, Sogandares-Bernal, Eldred, Ingle, and Woodburn, 1959).

Several larval cestodes of the order Trypanorhyncha have been found in the digestive gland and other organs of shrimps. Larval *Prochristianella penaei* Kruse were identified from four species of shrimps—brown, pink, white, and humpback (*Trachypeneus constrictus* (Stimpson))—from the Florida coast (Sparks and

Mackin, 1957; Woodburn et al., 1957; Hutton, Sogandares-Bernal, Eldred, Ingle, and Woodburn, 1959; and Kruse, 1959a, 1959b). Aldrich (1965) found the same cestode larvae in *Penaeus aztecus* and *P. setiferus* from the Texas coast. The adult worm was identified from the Atlantic stingray *Dasyotis sabina* LeSueur. Another trypanorhynch larva, unidentified, was seen by Ward (1962) in great numbers in the abdominal muscles, gills, and pericardium of the white shrimp from the Gulf of Mexico.

Trypanorhynch larvae have been found in commercial shrimps from other parts of the world. Yamaguti (1934) reported larvae, probably *Tetrarhynchus rubromaculatus* Diesing, in *Penaeopsis* sp. from Japan. Heldt (1949) took a larval cestode resembling *Eutetrarhynchus ruficollis* (Eysenhardt) from *Penaeus trisulcatus* Leach from the North African coast.

Larval nematodes of the genus *Contracaecum* were found in Florida shrimps by Woodburn et al. (1957), Hutton, Sogandares-Bernal, Eldred, Ingle, and Woodburn (1959), and Kruse (1959b). Margolis and Butler (1954) observed adult nematodes, *C. aduncum,* in a single specimen of northern pink shrimp *Pandalus borealis* Krøyer from British Columbia, Canada.

Diseases Caused by Parasitic Crustaceans

Epicaridean isopods are well-known parasites of Crustacea, and several genera occur on shrimps. Baer (1951), for example, stated that the epicaridean *Hemiarthrus abdominalis* (Krøyer) had been recovered from 20 species of shrimps belonging to the genera *Pandalus* and *Spirontocaris.* Joseph Uzmann (personal communication, Jan. 31, 1967) has found *H. abdominalis* on northern pink shrimp from the Gulf of Maine. The parasite has also been reported on *P. borealis* from Greenland (Horsted and Smidt, 1956) but not from Norway or England (Dahl, 1949; Allen, 1966).

Ricketts and Calvin (1962) described the occurrence of the bopyrid isopod *Argeia pugettensis,* which caused unilateral protuberances of the carapace of the black-tailed shrimp, *Crago nigricauda* (Stimpson), from the Pacific coast of the United States. Infestation was estimated at 3 to 5 percent. Japanese "red prawns," *Penaeopsis akayebi* Rathbun, are frequently (up to 70 percent) infested with another bopyrid *Epipenaeon japonicus* Thielemann. Hiraiwa and Sato (1939) found the gonads of parasitized individuals reduced, or in some males, completely atrophied. Presence of the branchial parasite *Bopyrus squillarum* on the shrimp *Leander serrifer* causes suppression of the ovaries and the breeding characters of the pleopods (Yoshida, 1952).

Several rhizocephalans have been reported as parasites of shrimps. Potts (1912) described *Mycetomorpha vancouverensis* from *Crago communis* Rathbun, and Calman (1898) described *Sylon hippolytes* from the dock shrimp, *Pandalus danae* Stimpson, both from Puget Sound, Wash.

DISEASES AS A POSSIBLE CAUSE OF MASS MORTALITIES

Many physical, chemical, and biological variables contribute directly or indirectly to mortalities of commercially valuable marine invertebrates. Various environmental factors and some of their effects have been discussed by Dexter (1944), Brongersma-Sanders (1957), Coe (1957), Mackin (1961), Dickie and Medcof (1963), Medcof and Bourne (1964), and Merrill and Posgay (1964). It seems clear that the actual cause of death in many mass mortalities is often undetermined, even after exhaustive studies such as those of Orton (1924a, 1924b), who studied oyster mortalities in England in 1920–21, and Roughley (1926), who examined oyster mortalities in Australia in 1924–25.

Disease has often been suspected as a cause of mortalities, but the actual disease agent often has proved to be elusive. Hirsch (1921), Dollfus (1923), and Korringa (1952a) reported major mortalities of sea mussels, probably due to a contagious disease, in the period 1900–19. The mortalities reached a peak in 1914–16. Sick mussels lost their byssal attachment, mantles were retracted, meats were thin, and adductor muscles were weak. Histological and bacteriological examinations were inconclusive. Soon thereafter—1919–23—catastrophic mortalities of European oysters occurred in western Europe. Deaths began in 1919 in Mar Piccolo, near Taranto, Italy (Cerruti, 1941), and quickly spread to England and other European countries. Orton (1924a) suspected, but was unable to demonstrate, a bacterial pathogen. Although no infectious agent was directly associated with the mortalities, disease signs such as mantle retraction, pale digestive gland, muscle degeneration, and pustules on the shell and mantle were seen. Ulcerations and pustules on the body and mantle, and shell pustules containing dead or moribund leucocytes were observed in oysters from England and the Netherlands during periods of mortality (Orton, 1937). These signs often result from disease. The exhaustive studies of Orton were supplemented by those of Eyre (1923, 1924), who isolated a number of species of bacteria from sick and healthy oysters, but doubted that any were true pathogens.

Korringa (1952a) gave an excellent historical account of these mortalities of oysters in Europe. Cultured-oyster beds in France, England, Denmark, Germany, and the Netherlands were affected almost simultaneously. Many natural beds were also destroyed. A few isolated populations—Helgoland and Brittany—were not affected until several years later. Mortalities did not occur in Portuguese oysters during this time. Although environmental factors such as poor food supply and low temperatures were held by some to be causes of the catastrophic mortalities (Gaarder and Alvsaker, 1941; Spärck, 1950), the available evidence strongly indicates an infectious disease (Cole, 1951b; Fischer, 1951; Korringa, 1952a).

A mortality, with characteristics very similar to those seen in the European oyster, was described by Roughley (1926) in populations of rock oysters, *Crassostrea commercialis* (Iredale and Roughly), from Australia. Oysters died in 1924 and 1925 in Georges River, New South Wales. Disease signs, such as abscesses and ulcerations, were observed, and a bacterial pathogen was suspected—possibly combined with winter environmental stresses.

Disease-associated mortalities, with a history of long and frustrating scientific study, were first observed in 1915 in American oysters of Prince Edward Island, Canada (Needler and Logie, 1947). In the period 1915–33, the disease (commonly known as "malpeque disease") spread around the Island and destroyed most of the oyster stocks—some of which required 20 years to return to previous levels of abundance (Logie, 1956). During the outbreak, oysters apparently developed resistance to the causative organism, whose identity remains undetermined. Beginning in 1955, mortalities, probably due to the same disease, began in waters of the adjacent mainland of New Brunswick across Northumberland Strait. Oyster populations along the entire northern coast of New Brunswick and Nova Scotia were decimated, but mass transfer of disease-resistant oysters from Prince Edward Island waters, beginning in 1957, has hastened the recovery of the fishery (Logie, Drinnan, and Henderson, 1960; Drinnan and England, 1965).

Pacific oysters imported as seed from Japan and planted in waters of the States of Washington and California began to die in significant numbers in the late 1950's. Oysters in their second year after introduction were most commonly killed; peaks of mortalities occurred in late summer; and deaths were most often observed at the heads of bays. In the absence of other obvious environmental changes, and because of the selective nature of the mortalities, it seems logical to suspect disease. A pathological condition described by us as "focal necrosis," has been found in seed from Japan and in several samples of larger oysters from beds in Washington. As many as 30 percent of the individuals in a sample were affected. In addition, a haplosporidan parasite, morphologically similar to the pathogen *Minchinia nelsoni* associated with recent mortalities on the U.S. east coast, has been seen by staff members of the BCF Biological Laboratory, Oxford, Md., in Pacific oysters from the State of Washington; a similar organism was recognized recently in a sample of seed oysters from Taiwan. Pereyra (1964) mentioned a "multinucleated MSX-like organism, possibly pathogenic" in a dying oyster from Oyster Bay, Wash. No clear association has yet been made, however, of specific pathogens with mortalities of *C. gigas* on the Pacific coast of the United States, and it is quite possible that other environmental factors are operative in the mortality areas.

The Japanese literature contains numerous historical accounts of mass mortalities of oysters dating back to 1915. Although disease was often suspected, specific pathogens were usually not identified. Takeuchi et al. (1960) mentioned large-scale deaths of oysters in Kanasawa Bay, beginning in 1915 and continuing for a number of years. Over 80 percent of the oysters in that bay died annually. Ogasawara et al. (1962) reported similar mass mortalities on the Miura peninsula, beginning in 1927 and continuing for 10 years. Oyster farms along the coast of the peninsula lost 50 to 80 percent of their crop annually. More recent mortalities of 2-year-old oysters have occurred in Hiroshima Bay and adjacent localities, beginning in 1945 (Fujita et al., 1953). A 10-year study (Takeuchi, Matsubara, Hirokawa, and Tsukiyama, 1955, 1956; Takeuchi, Matsubara, Hirokawa, and Matsuo, 1957; and Takeuchi et al., 1960) provided somewhat inconclusive evidence that a bacterial pathogen was responsible for the mortalities.

A series of papers by Tohoku Regional Fisheries Research Laboratory (Imai et al., 1965; Kan-no et al., 1965; Mori, Imai, Toyoshima, and Usuki, 1965; Mori, Tamate, Imai, and Itikawa, 1965; Numachi et al., 1965; Tamate et al., 1965) described mass mortalities of oysters in Matsushima Bay, Miyagi Prefecture, Japan, that have occurred annually in late summer since 1961. Environmental, physiological, and pathological factors were examined. Pathological changes were observed, and mortalities were considered to be related to metabolic changes during fattening and spawning. Mortalities exceeded 60 per cent per year in certain areas of the Bay during 1961–64. A gram-positive bacterium was found in multiple abscesses in as many as 20 percent of oysters in certain samples (Numachi et al., 1965), but a causal relation with mortalities was not established. Our later studies suggest that the disease condition is the same as that called "focal necrosis" in adult Pacific oysters from Washington. The pathogen warrants further observation, since the abscesses may represent only the chronic stage of infection in resistant hosts, whereas the acute disease may have a significant effect on mortality. An ameboid organism, often present in large numbers and accompanied by pronounced host response, has also been found in oysters from the Matsushima Bay mortality area.

Blue crab populations on the coasts of North and South Carolina have been affected by extensive mortalities beginning in 1965 (Lunz, 1967). Significant impact on population size was indicated by a marked drop in catch per unit effort in 1966, as compared with the previous 5 years. Newspapers stated that great numbers of crabs were washed up on beaches or littered the bottoms of creeks, and that catches were drastically reduced. Disease has been suspected (Lunz, 1967), but no clear evidence of a pathogen has been obtained. Such mortalities in wild crabs are apparently distinct from the long-recognized high levels of deaths in crab shedding floats (Beaven and Truitt, 1939), which may in part be associated with parasites or diseases (Couch, 1966; Sprague and Beckett, 1966).

A few mass mortalities of marine invertebrates have been definitely ascribed to epizootics caused by specific pathogens (Sindermann, 1963). Recurring mortalities of American oysters in the Gulf of Mexico were found to be caused by the fungus *Dermocystidium marinum*. Exerting its effects in higher salinities and temperatures among dense aggregations of hosts, the pathogen can cause annual mortalities in excess of 50 percent. Development and use of a presumptive test, with thioglycollate medium (Ray, 1952), has established the presence of the organism in oysters throughout the Gulf of Mexico and northward along the Atlantic coast as far as Connecticut. Although the fungus may at times reach epizootic levels in particular areas, its most significant effect is probably that of continuing attrition, year after year, during periods of high sea-water temperature. Effects of the disease on commercial beds are now controlled to some extent by planting and harvesting at prescribed times of the year and by spreading oysters thinly on the beds.

Major mortalities, with consequent severe depression of the oyster fishery, occurred in Delaware and Chesapeake Bays on the U.S. east coast, beginning in the late 1950's. A haplosporidan parasite with distinctive characteristics, *Minchinia nelsoni*, has been associated with the mortalities. Epizootic areas have had oyster losses in excess of 90 percent, and some indications are appearing of increased resistance among survivors. The disease, like that caused by *Dermocystidium*, exists and exerts severe effects in salinities above 15 o/oo. Seed beds and oyster stocks in low-salinity areas have not been destroyed. Recently the organism has been found in oyster populations on the coasts of New York and North Carolina—well outside previous areas of high mortality.

Studies of these serious pathogens of oysters —*D. marinum and M. nelsoni*—have revealed the very important role of a "salinity barrier" to certain diseases. The fungus *D. marinum* exerts severe effects on oyster populations in high-salinity waters of the Gulf of Mexico but does not flourish in low-salinity areas. *M. nelsoni,* which has seriously affected oyster stocks of the Middle Atlantic States, also occurs in higher salinities. Both pathogens seem confined to salinities above 15 o/oo; this fact has made possible the continuation of production in parts of coastal areas affected by these epizootics.

Inhibitory effects of low temperature have been well illustrated for these serious oyster pathogens. *D. marinum* causes warm-weather mortalities in American oysters; in fact, the plantings of seed oysters are timed to take advantage of the relative quiescence of the disease in cooler seasons. Surveys of *Dermocystidium* have indicated marked decline in winter. *M. nelsoni,* of Chesapeake Bay and Delaware Bay, is similarly quiescent in winter. New infections are not apparent, prevalence of disease declines, existing infections seem less active, and mortalities are reduced.

Mackin (1961) attempted, from a review of the literature, to itemize characteristics of mortalities of oysters due to various causes. As one who has published extensively on the role of disease in oyster populations, he naturally turned his attention toward mortalities caused by infectious agents. Among many interesting comments in his paper, Mackin stated that "all oyster producing bays are endemic areas for one or more diseases" and that "not only are bivalve mollusks frequent hosts for pathogens, but they are regularly parasitized by a unique group of low fungi." Mackin further stated his belief that "of all causes of mortality, disease ranks first." Disease, then, can cause significant, if temporary, reductions in population abundance of marine invertebrates. Such reductions may exceed 95 percent of existing stocks. Additionally, there is every indication that serious but undescribed diseases exist among marine invertebrates. Mackin (1962), for example, mentioned a number of pathological conditions in oysters that were not associated with known pathogens. Rust disease of Pacific king crabs, which we have described on the basis of an unpublished report, is a commonly recognized condition in the fishery, but has not been described in the published scientific literature.

Destruction of most of a population by epizootics and mass mortalities, of course, also reduces pathogen numbers, because the possibility of finding a new susceptible host at a critical point in the life cycle is reduced.

Less spectacular mortalities, which also have severe continuing depressive effects on host population size, are probably more common than large-scale or mass mortalities. Minor fluctuations in abundance may be attributable to such "background" mortalities. Also, those parasites and diseases that do not kill the host may act as indirect agents of mortality. Abnormal individuals are rendered more vulnerable to predation in many ways: their body muscles may be partially destroyed, covering or erosion of their gills may interfere with respiration, or their normal protective coloration may be modified or obscured. For example, Hopkins (1957a) has observed that blue crabs prey more frequently on oysters which cannot close their shells as quickly or as tightly as normal oysters. Any increase in parasite burden must reduce the probability of survival in an environment where death, early and sudden, is the rule rather than the exception. For parasites with complex life cycles involving two or more hosts, consumption of an earlier host in the cycle—one weakened by the parasite—by the right predator may be critical to the completion of the cycle.

Another prominent effect of parasitization of marine mollusks and crustaceans is sterilization of the host. Larval trematodes are notable for destroying the gonads of gastropods and bivalves, and parasitic barnacles and certain isopods produce similar effects in crustaceans. In areas where levels of parasitization are high, the reproductive capacity of the host population may be seriously impaired. In a study of the ecological relation of the marine snail, *Littorina littorea,* and its trematode parasite, *Cryptoctyle lingua,* Sindermann and Farrin

(1962), and Sindermann (1965, 1966a) found prevalences of the parasite of over 50 percent in certain coastal areas, indicating that the reproductive potential of snail populations was suppressed by that amount. An excellent review of parasitic castration of Crustacea has been provided by Reinhard (1956).

Effects of disease can be generally categorized as catastrophic, resulting in mass mortalities, or continuing, producing a constant drain on population numbers. Although disease is always with us, and mortalities have undoubtedly occurred in the past, new factors have been introduced by man to set the stage for the spread of epizootic disease. For example, oysters are transferred promiscuously from one geographic area to another; populations are often crowded in dense beds, sometimes in areas where natural populations did not exist previously; drastic physical and chemical changes have been made in oyster habitats; and new predators have been introduced. A dominant mortality factor—disease—has been aided by human activities; it must be controlled, if we are to achieve maximum production of cultivated inshore mollusks and crustaceans.

Many different environmental factors—physical, chemical, and biological—can kill oysters, crabs, or other animals of commercial value (Brongersma-Sanders, 1957). Any single factor may become overriding, however, at a particular time in the life of a species—and in this paper we have described several examples of how the factor of disease can reduce the abundance of marine species.

It is easy, of course, to overextend any point of view; we do not imply here that every decrease in abundance can be blamed on disease. An excellent case could also be made from the published literature for the significant role of predation—particularly during population peaks of particular predator species—as a major cause of fluctuations in abundance of commercially valuable species. Man-made changes in environment can also affect abundance. Because of industrial pollution, shellfish populations have been eliminated from certain localized areas within estuaries and along the coast. In addition, other types of pollution have made extensive areas in rivers and bays unavailable for the harvesting of shellfish. It is likely that mass mortalities are, and have always been, natural methods of population regulation—but, until recently, these mortalities would have been accepted with the same dazed bewilderment and inaction that must have characterized the behavior of our ancestors during the plagues of the dark ages. We can now look to methods of environmental control and stock manipulation, particularly for sedentary shallow water species such as oysters, clams, and even certain Crustacea, as part of the methodology of an increasingly complex system of cultivation of our inshore waters.

CONTROL OF DISEASES OF MARINE INVERTEBRATES

The original, persistent, and largely erroneous feeling about disease in marine populations is that little can be done about it. This pessimistic attitude is definitely unwarranted for species that live inshore—particularly the sedentary invertebrates—where practical measures of disease control are possible and have already been applied in some situations. Possible methods include the following:

1. *The transfer of susceptible animals into epizootic areas, or of individuals from such areas, should be prevented.* Because each disease is discrete in terms of transmission and infectivity, risks of transfer will vary as well. When intermediate or alternate hosts play a significant role in maintaining the disease in a given geographic area, transfer of infected individuals to other areas where these hosts are absent may be a reasonable management procedure. Diseases that have been demonstrated experimentally to be transmitted directly, however, such as *Dermocystidium* infections of oysters, may be maintained at epizootic levels by repeated introduction of susceptible animals.

2. *Disease-resistant stocks should be developed by selective breeding of survivors.* Epizootics of several oyster diseases have apparently produced increased resistance among survivors. During the outbreak of "malpeque disease" in Prince Edward Island (Canada) oysters, resistance developed to an unidentified pathogen, and stocks returned to previous levels of abundance after several decades. That the pathogen is still present is indicated by deaths of suscep-

tible oysters from other geographic areas introduced into Prince Edward Island waters. Resistant stocks were drawn upon to repopulate other oyster growing areas of the Gulf of Saint Lawrence that had been subsequently decimated by the same disease.

Evidence is accumulating that increased resistance to the haplosporidan pathogen *Minchinia nelsoni* is developing among oysters that have survived the disease in the Middle Atlantic States. The disease has been at epizootic levels in some Chesapeake Bay populations for several years. Perhaps resistant strains can be developed with presently available hatchery techniques. Aggregation of survivors on natural beds to which adequate cultch has been added could also do much to improve reproduction, spatfall, and return to full production.

3. *Basic information about the life history and ecology of the disease agent must be accumulated, to define vulnerable stages or restrictive environmental requirements.* As an example, several oyster pathogens, such as *M. nelsoni,* are limited to salinities in excess of 15 o/oo. Plantings during epizootics can be restricted to low-salinity areas, and temporary transfer of infected stocks to low salinities may retard or eliminate infections. Mechanical and chemical treatments can also reduce disease prevalence. Effects of gaffkaemia on impounded lobster populations have been reduced by treating bottom muds of pounds with calcium hypochlorite. Damages of dermocystidium disease to oysters have been lessened by planting oysters thinly on the beds, by harvesting within 2 years, and by planting and harvesting at prescribed seasons to take advantage of the decrease in pathogen activity during the colder months.

Korringa (1959) outlined an extensive program to control the spread of the parasitic copepod *Mytilicola* in cultivated mussel stocks of the Netherlands. Included were extensive dredging of adjacent natural beds, transfer of lightly infested stocks, and destruction of heavily infested beds.

Korringa (1951a) found "shell disease" of oysters to be caused by a fungus that perforated the shell—a fungus that thrived on old shells. He attributed the outbreak of shell disease in 1930 in the Netherlands to the practice of spreading enormous quantities of cockle shells on the beds. The disease declined when the spat collectors were placed in areas free of the disease, when old shells were cleared from beds, and when infected young oysters were dipped in mercuric disinfectant (Korringa, 1948, 1949, 1951c).

Biological control of other hosts in the life cycle of parasites, or biological control of the parasite itself, are also possible approaches.

4. *Production could be maintained in artificial environments where disease can be controlled.* Some progress has been made in this direction with the development of hatchery methods of producing seed oysters and clams (Loosanoff and Davis, 1963). Bacterial and fungal epizootics in larval culture tanks can be prevented, or their effects reduced, by ultraviolet treatment of filtered sea water, antibiotic treatment of sea water in standing water cultures, maintenance of general cleanliness of all utensils used in handling larvae, and ultraviolet treatment of phytoplankton food derived from impure mass cultures.

Shellfish production in artificial ponds (Shaw, 1965) offers distinct possibilities of disease and predator control, beginning with disease-free and disease-resistant brood stock and progressing to filtration and ultraviolet treatment of recirculated water; important also are careful control of contaminants in mass phytoplankton cultures and elimination of shellfish associates that act as alternate or intermediate hosts of disease agents.

CONCLUSIONS

Many of the great fisheries of the world have undergone large fluctuations in supply. The causes of these fluctuations, although subjects of much discussion, have rarely been precisely determined. Reduction in abundance of commercially valuable marine species has been attributed to overfishing, failure of spawning, sudden and drastic changes in temperature and salinity, and many other factors. One biological factor that has received too little attention is disease. The fact that marine animals become ill and die, often in vast numbers, has been largely ignored. Events in commercial shellfish populations in this century, however, have forced us to look closely at disease as a cause of mass mortalities of epic proportions, and of subsequent major declines in abundance of commercial species.

Molluscan and crustacean species of economic value as food have been affected by diseases, some of which have produced epizootics with resultant mass mortalities. Much attention has been directed toward oyster diseases, possibly because oysters have been cultivated more intensively than most other inshore or estuarine species. Microbial diseases—including those of bacterial, fungal, and protozoal etiology—have affected oyster stocks in many parts of the world. Bacterial diseases have had serious effects on lobsters, and a number of Protozoa, particularly Microsporida, affect crab and shrimp populations.

It is often difficult to establish the precise cause of death of marine invertebrates—to determine whether a suspected pathogen is a primary or secondary invader. Environmental and physiological factors can be inextricably associated with apparent disease; their relative effects are often not easy to assess. Thus, the literature on mass mortalities contains measurements of many environmental variables, descriptions of physiological conditions of host animals, and reports of suspected disease agents—but too frequently the studies have been unable to point to a single cause of death. The search for a single cause may have been an oversimplified approach to a complex problem. In other situations, epizootics of specific pathogens, possibly influenced to some extent by environmental factors, can be directly related to the state of resistance of the host population, the virulence and infectivity of the pathogen, and infection pressure.

Mass mortalities, many of undetermined causes but some definitely the result of disease, have occurred in commercial invertebrate populations. These mortalities are a natural method of regulating population size; they have received increasing scrutiny in recent years. The development of methods of cultivation and of limited manipulation of the inshore environment should make it possible to reduce or eliminate the serious threat of disease to populations of commercial shellfish.

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SOME FEATURES OF THE GULF STREAM OFF CHESAPEAKE BAY IN THE SPRING OF 1963[1]

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ABSTRACT

Oceanographic measurements in May and June 1963, showed that water mixing was intense though intermittent at the western boundary of the Gulf Stream. Warm, saline water became separated from the Stream and mixed with the slope water as a result of divergence near the surface and upwelling. Data from repeated sections along three transects of the Gulf Stream are analyzed and presented in 22 cross-sectional plots. These plots show that a zone of intense mixing appeared intermittently at the western side of the Gulf Stream in an apparently fluctuating manner. Separation of this mixing zone from the Gulf Stream resulted from local ascent of cool water from the subsurface levels where there was a zone of steeply sloping isotherms. The results suggest that part of the mixed, dense water sank to about 200 m. below the depth at which it was produced and returned to the Gulf Stream.

Data for this report were obtained during Cruise 1 of the Bureau of Commercial Fisheries research ship *Geronimo* (May 8 to June 7, 1963). Although the primary purpose of the cruise was to test the ship and its gear, extensive physical and biological oceanographic observations were also made. The principal physical investigation was a study of the properties of the Gulf Stream along three transects described as follows (fig. 1):

> Transect I—16 sections across the left (inshore or western) boundary of the Gulf Stream—12 with bathythermograph observations only, and 4 with oceanographic stations (Nansen bottle casts) and BT's.
>
> Transect II—four sections across the left boundary (all with oceanographic stations and BT's).
>
> Transect III—three sections across the left boundary (all with oceanographic stations and BT's).

Most of the data used in this report were gathered by repeated occupation of these transects. For each transect, one section was extended southeastward into the Sargasso Sea. The right (offshore or eastern) boundary of the Gulf Stream was crossed six times.

Bathythermograph observations were taken every 5 nautical miles (9.3 km.), except that on a supplementary run from transect II to transect I along the left boundary, BT's were taken every 10 miles (18.5 km.). Observations at the oceanographic stations were limited to the upper 600 m. The last one or two digits in the numbers of the hydrographic station locations used in this report (fig. 1) indicate their chronology.

Continuous records of surface temperature were made with a Foxboro[3] thermograph and were checked by measurements with two thermistors and one bucket thermometer at the location of each BT observation. Portions of the Foxboro temperature records are reproduced (figs. 2 and 3 to 25). The lower trace on the temperature record is used when the upper trace exceeds the scale and is usually set 10° C. below the upper. The lower trace was not well controlled during this study, and the difference at times exceeds 10° C.

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[3] Trade names referred to here do not imply endorsement of commercial products.

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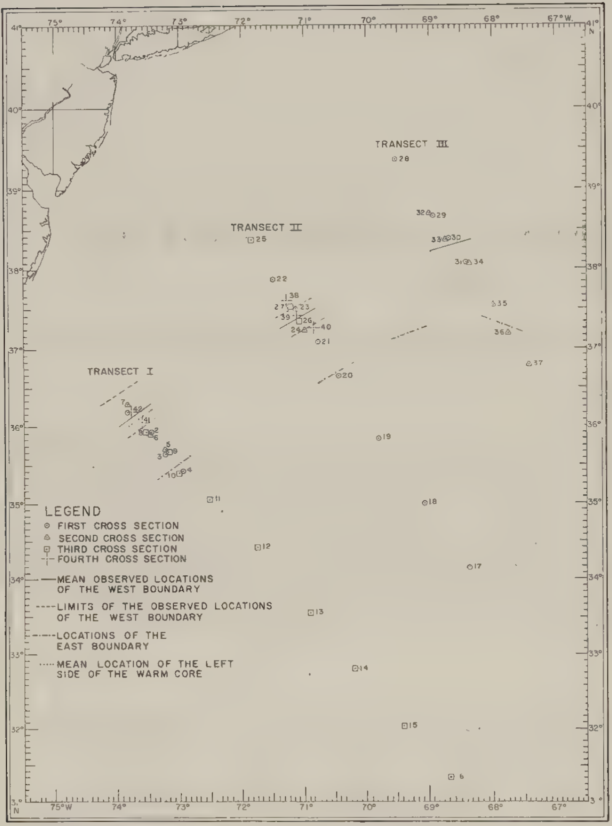

TRANSECT III
TRANSECT II
TRANSECT I
LEGEND
FIRST CROSS SECTION
SECOND CROSS SECTION
THIRD CROSS SECTION
FOURTH CROSS SECTION
MEAN OBSERVED LOCATIONS OF THE WEST BOUNDARY
LIMITS OF THE OBSERVED LOCATIONS OF THE WEST BOUNDARY
LOCATIONS OF THE EAST BOUNDARY
MEAN LOCATION OF THE LEFT SIDE OF THE WARM CORE
75°W
74°
73°
72°
71°
70°
69°
68°
67°
41°N
40°
39°
38°
37°
36°
35°
34°
33°
32°

FIGURE 1.—Locations of transects and (oceanographic) stations of R.V. *Geronimo* Cruise 1.

Continuous representation of the Gulf Stream structure along its axis is not possible because the observations were concentrated on transect lines about 140 miles (259.4 km.) apart. The detailed observations along each line do reveal a number of common properties among the transects. Most sections extend across only the left boundary of the Gulf Stream; therefore, my main intent is to interpret some variable and transient features of that boundary.

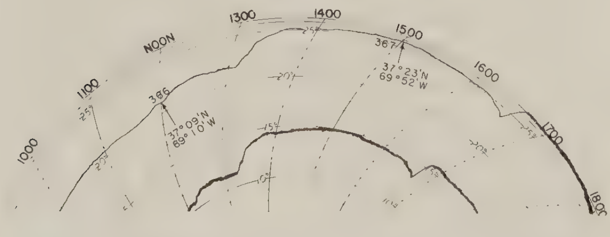


FIGURE 2.—Thermograph record of surface temperature change across the right boundary of the Gulf Stream between transects II and III. Temperatures greater than 25° C. are read from the lower of the two traces by adding 10° C. to the individual values. Bathythermogram numbers and locations are indicated along the temperature trace.

BOUNDARY SYSTEM

In defining the boundary system, I will describe the temperature structure in the area between the slope water and the Sargasso Sea.

SLOPE WATER—INTERMEDIATE WATER BOUNDARY

From the slope water to the Gulf Stream, the surface temperature increased in two steps along most of the sections. In a typical case (fig. 10), the first step was a positive gradient of about 8° C. in less than 1 mile (1.9 km.); this temperature increase was the offshore (eastern) boundary of the slope water. Beyond this first step was a rather wide intermediate area of very irregular surface temperatures. Another steep, positive surface gradient of about 4° to 6° C. was at the left boundary of the Gulf Stream; in most sections this gradient was above or slightly left of the zone of steeply sloping isotherms in the subsurface layers. Iselin (1936) reported similar observations of the slope water and Gulf Stream boundaries.

INTERMEDIATE ZONE

The width of the intermediate zone—between the offshore slope water and the inshore Gulf Stream boundaries—varied greatly. At times it was not observed at all; at other times it was as wide as 60 miles (111.1 km.). For example, the zone is practically nonexistent in figure 5, where surface temperature increased from 12° to 22° C. in about 3 miles (5.6 km.), followed by an increase of only about 2° more in the next 20 miles (37 km.) (the distance to the warm core). A contrasting situation is illustrated in figure 18, in which the intermediate zone is about 50 miles (92.6 km.) wide and the warm core of the Gulf Stream is immediately to the right of the Gulf Stream boundary.

LEFT BOUNDARY OF THE GULF STREAM

The left boundary of the Gulf Stream is defined here as the first strong thermal gradient crossing at the surface from the Gulf Stream toward the slope water. The mean location of

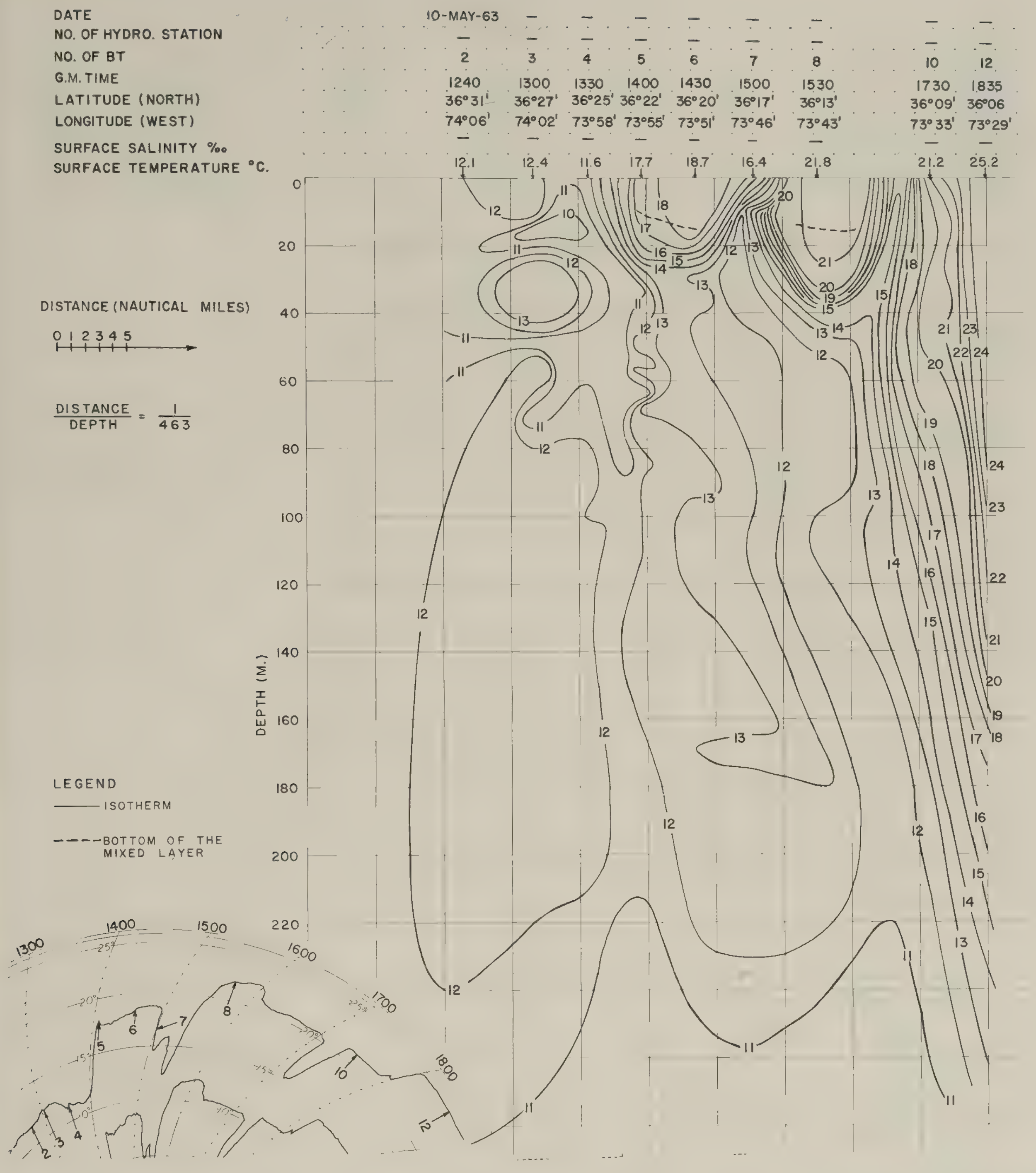


FIGURE 3.—Transect I—Section 1, May 10, 1963. Vertical temperature profile and thermograph record of surface temperatures. Thermograph temperatures greater than 25° C. are read from the lower of the two traces by adding 10° C. to the individual values. Bathythermogram numbers appear along the surface temperature trace to show the time of the casts.

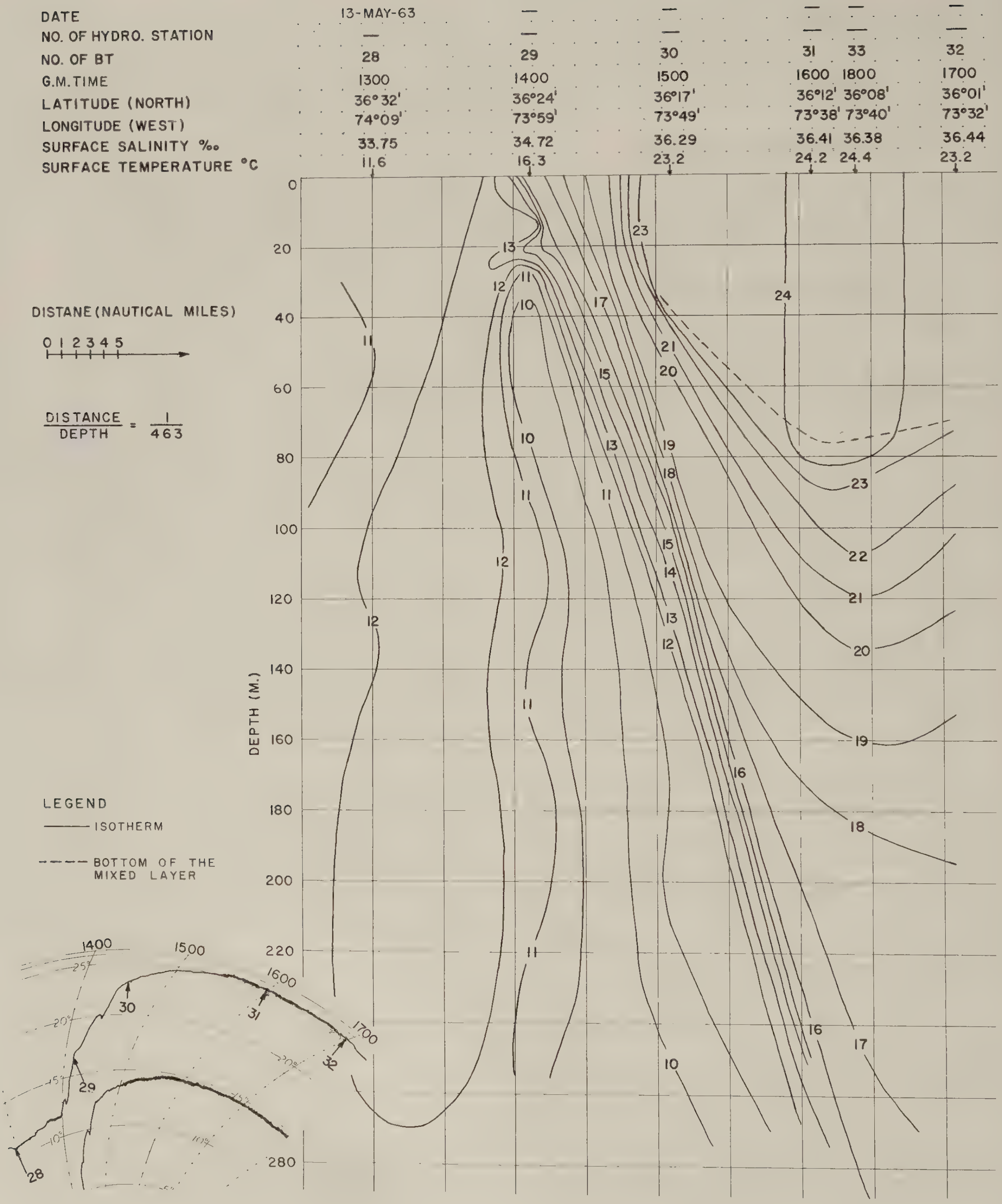


FIGURE 4.—Transect I—Section 2, May 13, 1963. (*See* caption for fig. 3.)

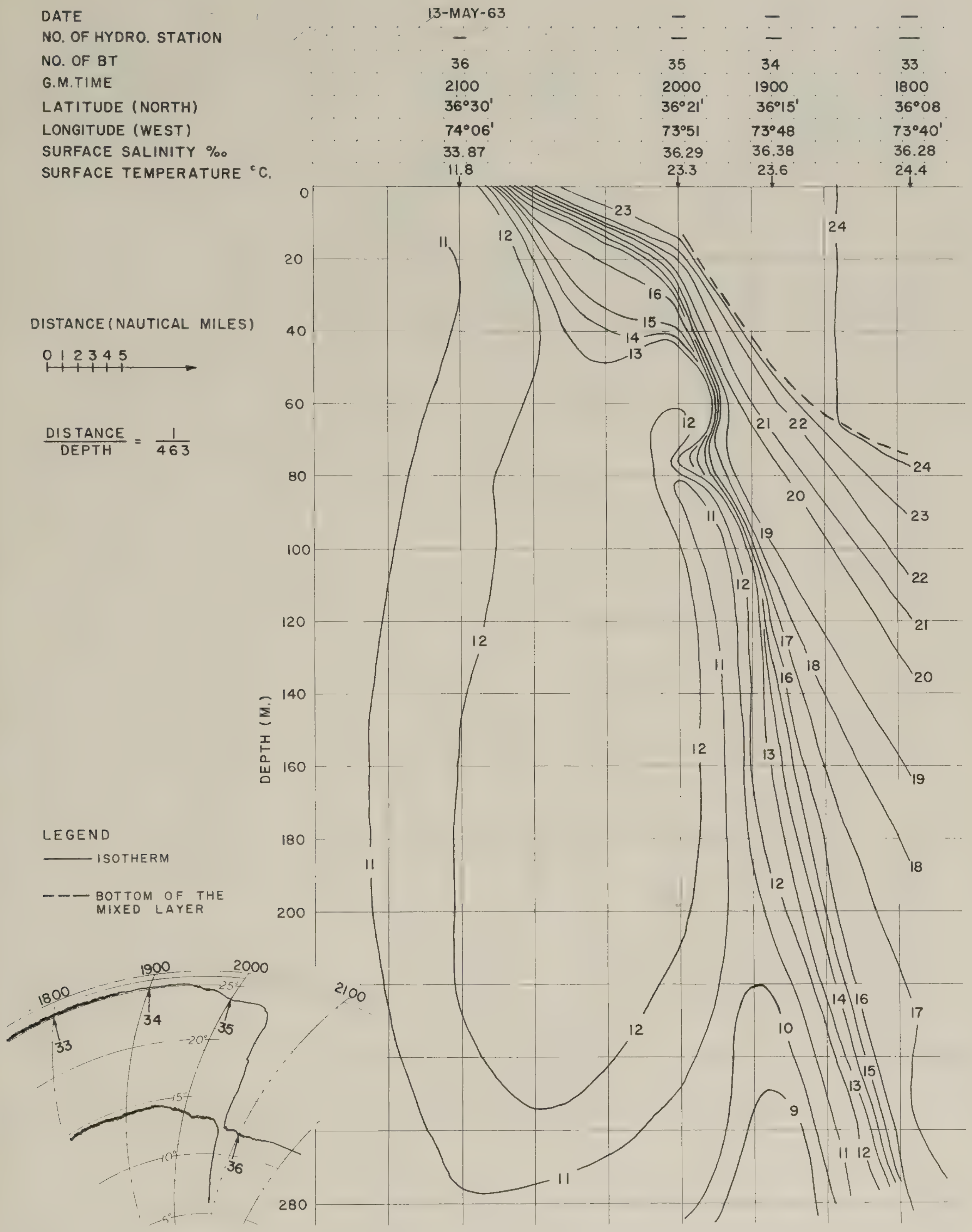


FIGURE 5.—Transect I—Section 3, May 13, 1963. (*See* caption for fig. 3.)

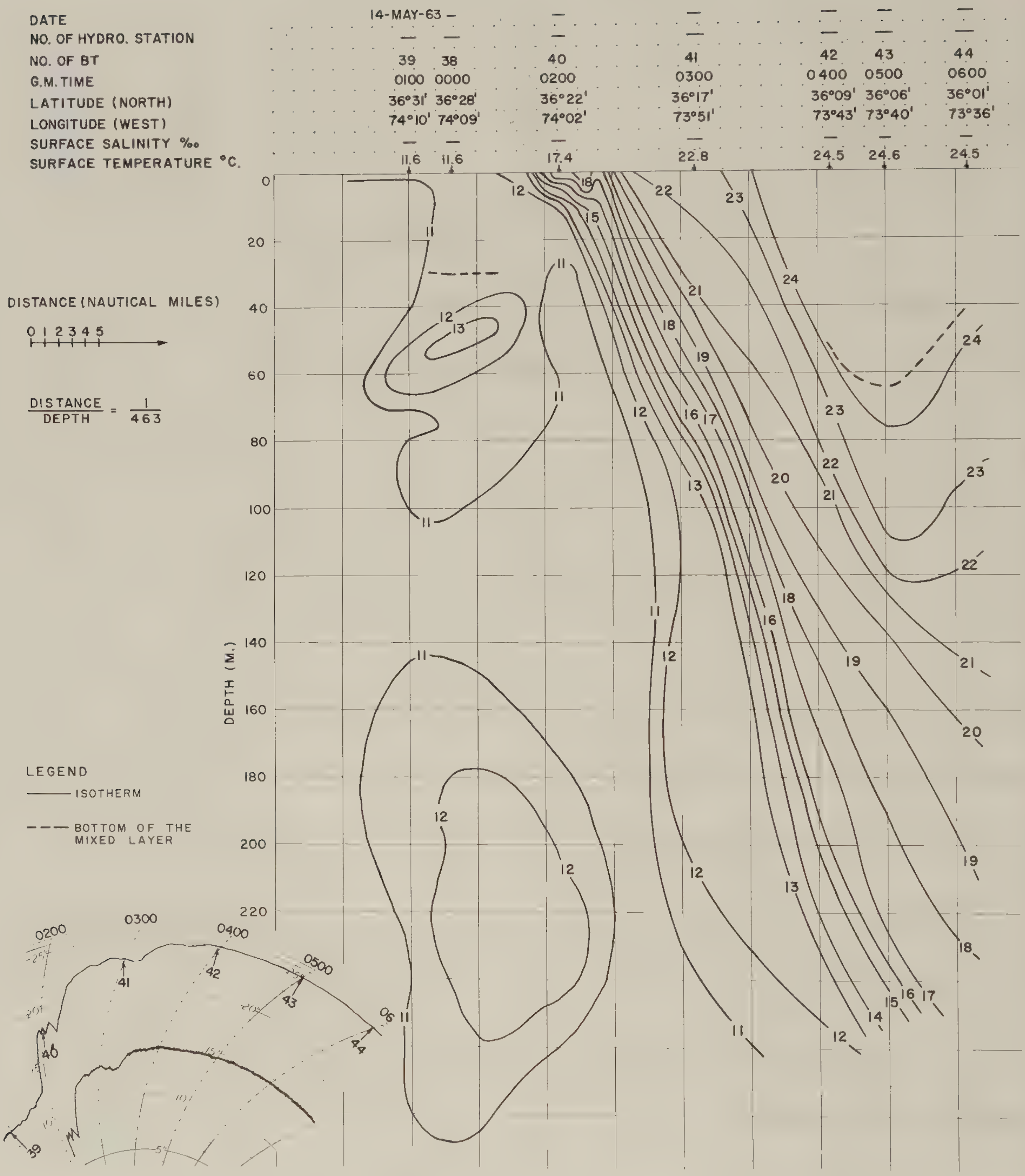


FIGURE 6.—Transect I—Section 4, May 14, 1963. (*See* caption for fig. 3.)

DATE	14-MAY-63	—	—	—	—
NO. OF HYDRO. STATION	—	—	—	—	—
NO. OF BT	49	48	47	46	45
G.M. TIME	1100	1000	0900	0800	0700
LATITUDE (NORTH)	36°30'	36°26'	36°19'	36°15'	36°07'
LONGITUDE (WEST)	74°10'	74°04'	73°54'	73°50'	73°40'
SURFACE SALINITY ‰	33.74	33.94	—	36.31	—
SURFACE TEMPERATURE °C.	11.3	11.6	21	24.7	24.6

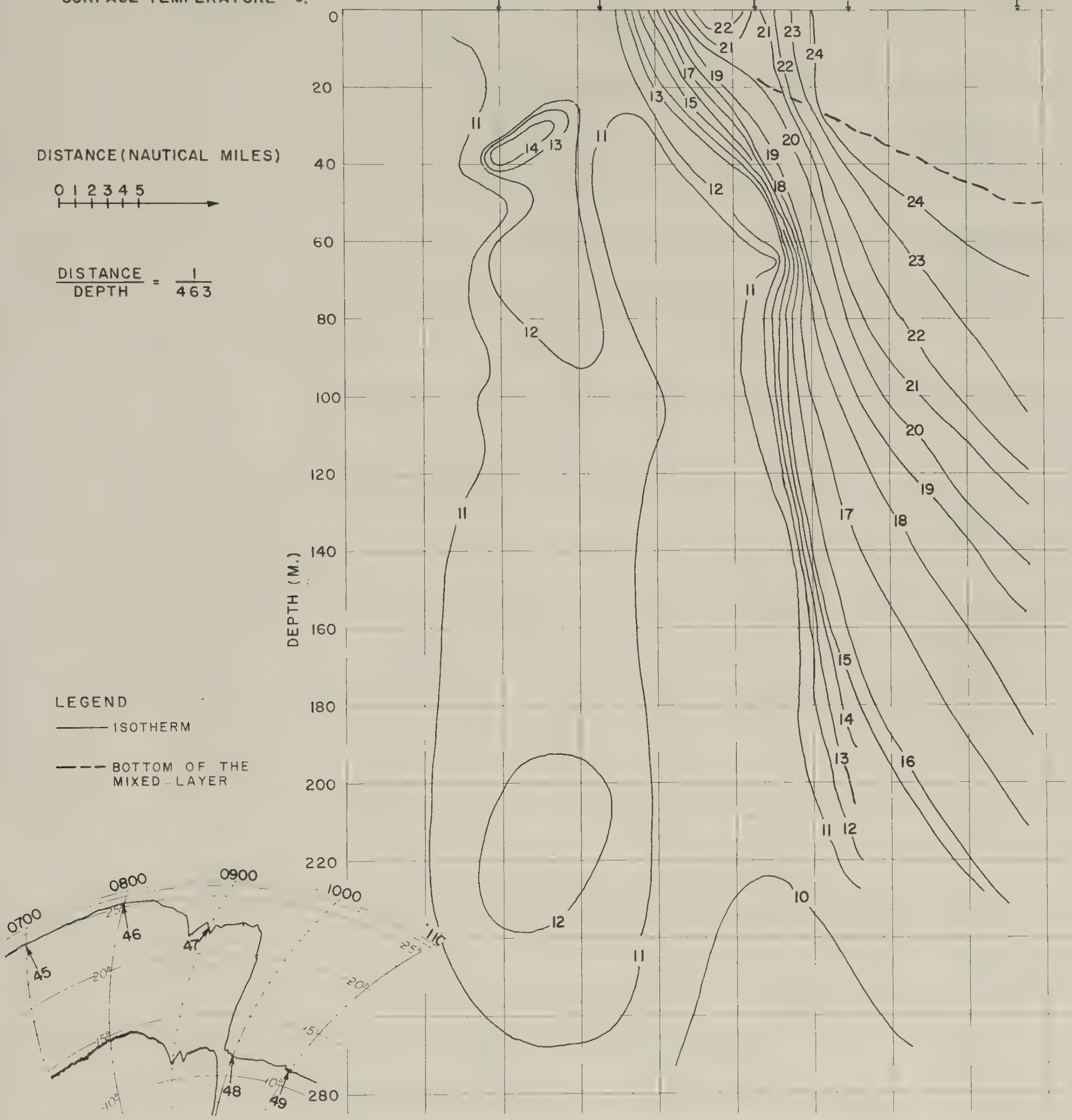


FIGURE 7.—Transect I—Section 5, May 14, 1963. (*See* caption for fig. 3.)

DATE	14-MAY-63	—	—	—	—	—	—	—	15-MAY-63	—
NO. OF HYDRO. STATION	—	—	—	—	—	—	—	—	—	—
NO. OF BT	50	51	52	54	56	57	58	61	65	66
G.M.TIME	1200	1300	1400	1600	1700	1800	1900	2200	0200	0300
LATITUDE (NORTH)	36°28'	36°20'	36°14'	36°12'	36°10'	36°08'	36°07'	36°06'	36°04'	36°00'
LONGITUDE (WEST)	74°06'	73°56'	73°48'	73°43'	73°40'	73°39'	73°39'	73°38'	73°38'	73°33'
SURFACE SALINITY ‰	33.89	36.17	36.13	36.42	36.42	—	36.42	36.37	36.04	36.36
SURFACE TEMPERATURE °C.	11.6	20.8	24.4	24.7	24.3	24.7	24.7	25.3	23.7	25

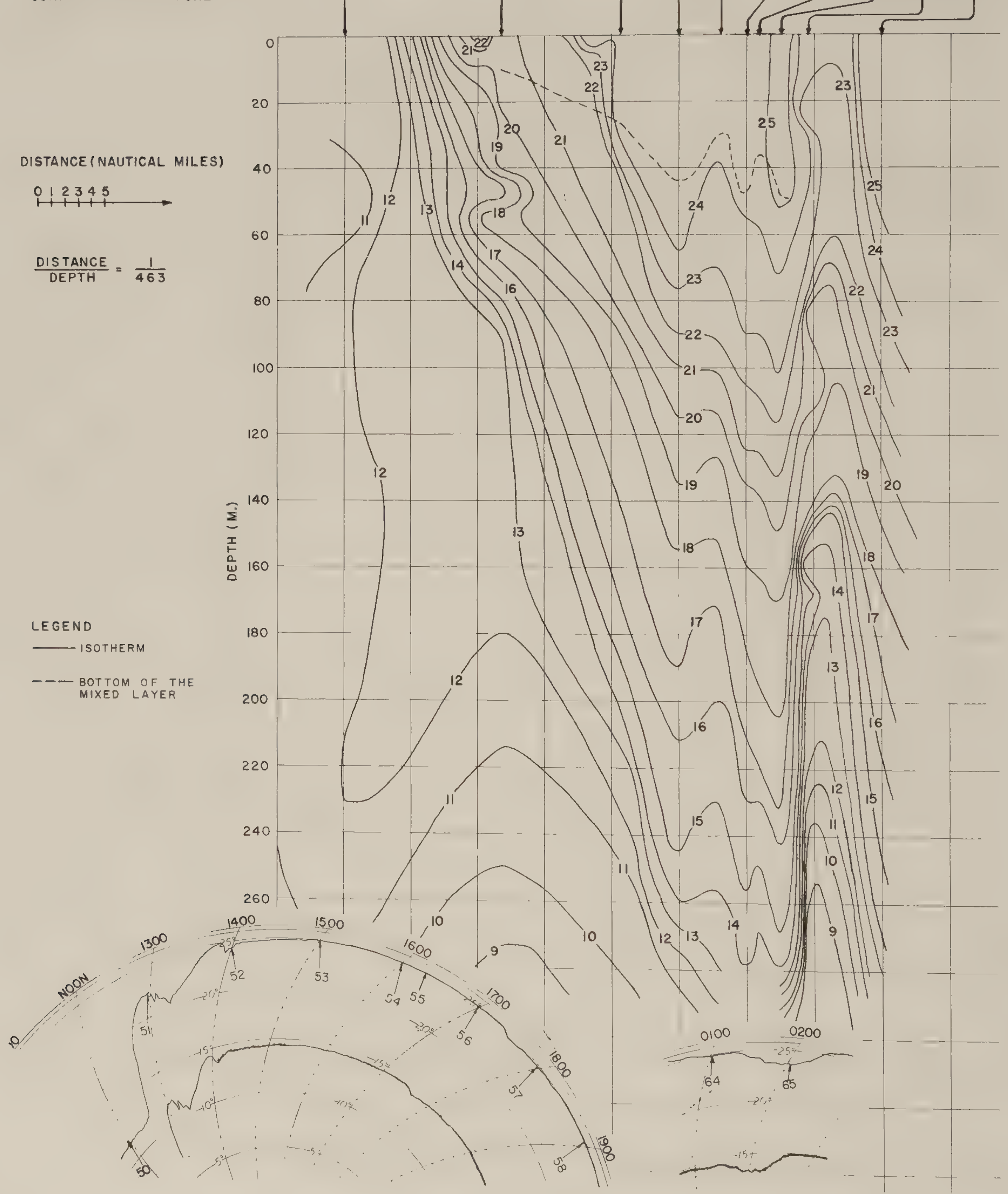


FIGURE 8.—Transect I—Section 6, May 14, 1963. (*See* caption for fig. 3.)

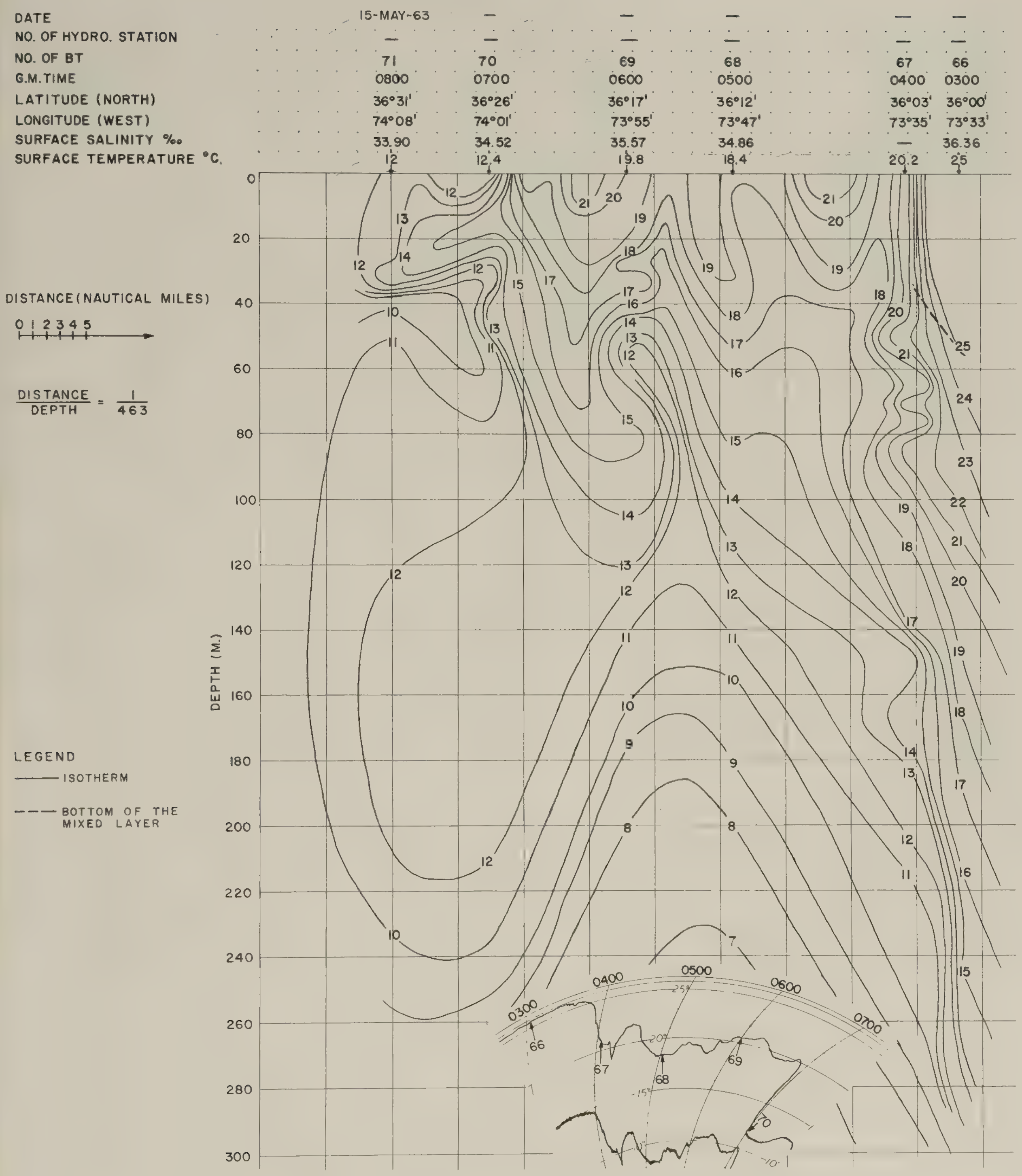


FIGURE 9.—Transect I—Section 7, May 15, 1963. (*See* caption for fig. 3.)

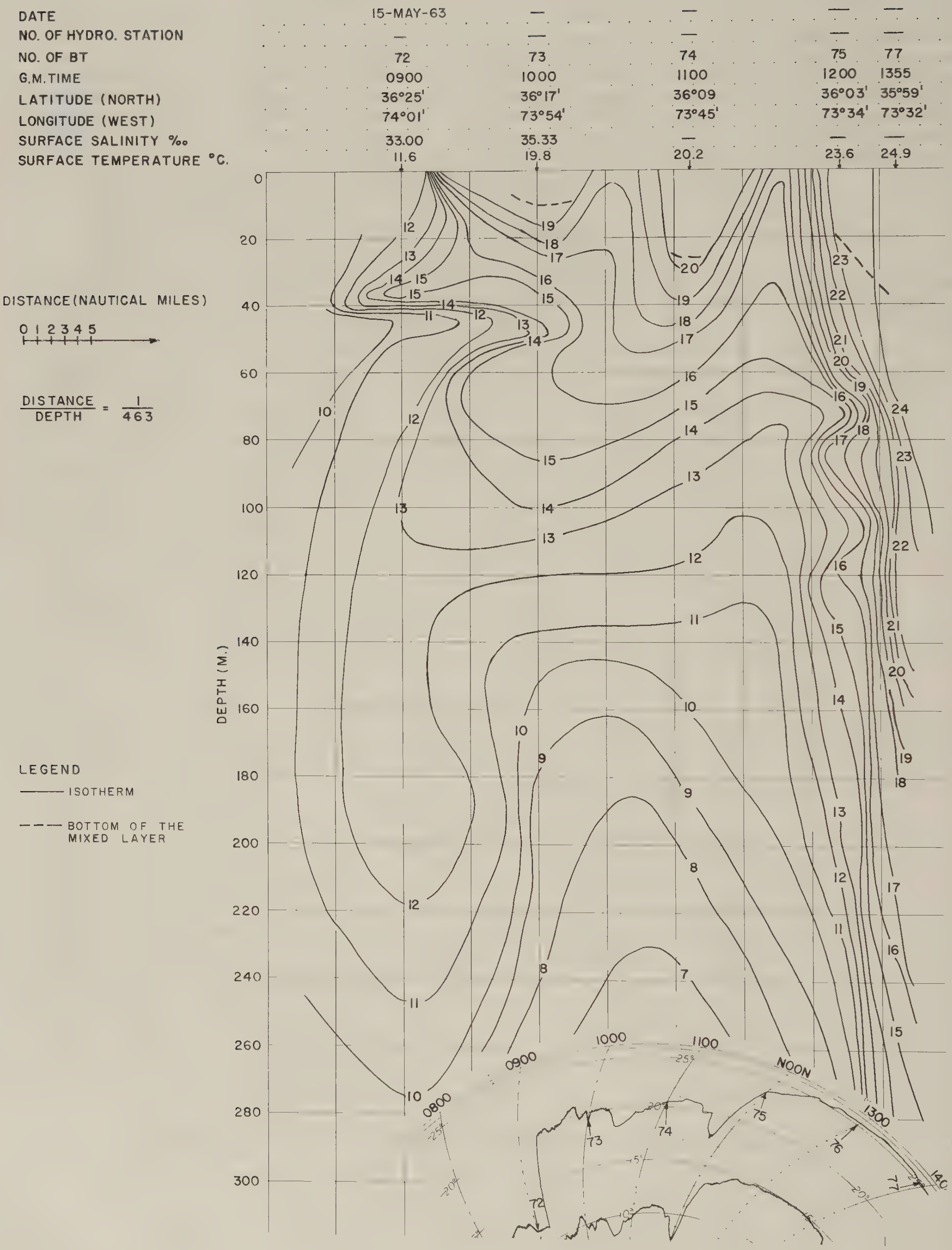


FIGURE 10.—Transect I—Section 8, May 15, 1963. (*See* caption for fig. 3.)

DATE	16-MAY-63	—	—	—	—	—	—	—
NO. OF HYDRO. STATION	—	—	—	—	—	—	—	—
NO. OF BT	96	93	92	89	88	87	86	84
G.M. TIME	1800	1000	0907	0600	0500	0400	0300	0605
LATITUDE (NORTH)	36°28′	36°22′	36°18′	36°16′	36°13′	36°09′	36°04′	35°57′
LONGITUDE (WEST)	74°23′	74°13′	74°05′	74°01′	73°54′	73°42′	73°31′	73°27′
SURFACE SALINITY ‰	33.15	34.14	35.36	35.14	36.07	35.53	36.39	—
SURFACE TEMPERATURE °C.	11.6	13.6	19.2	19.8	20.2	19.4	25.2	24.7

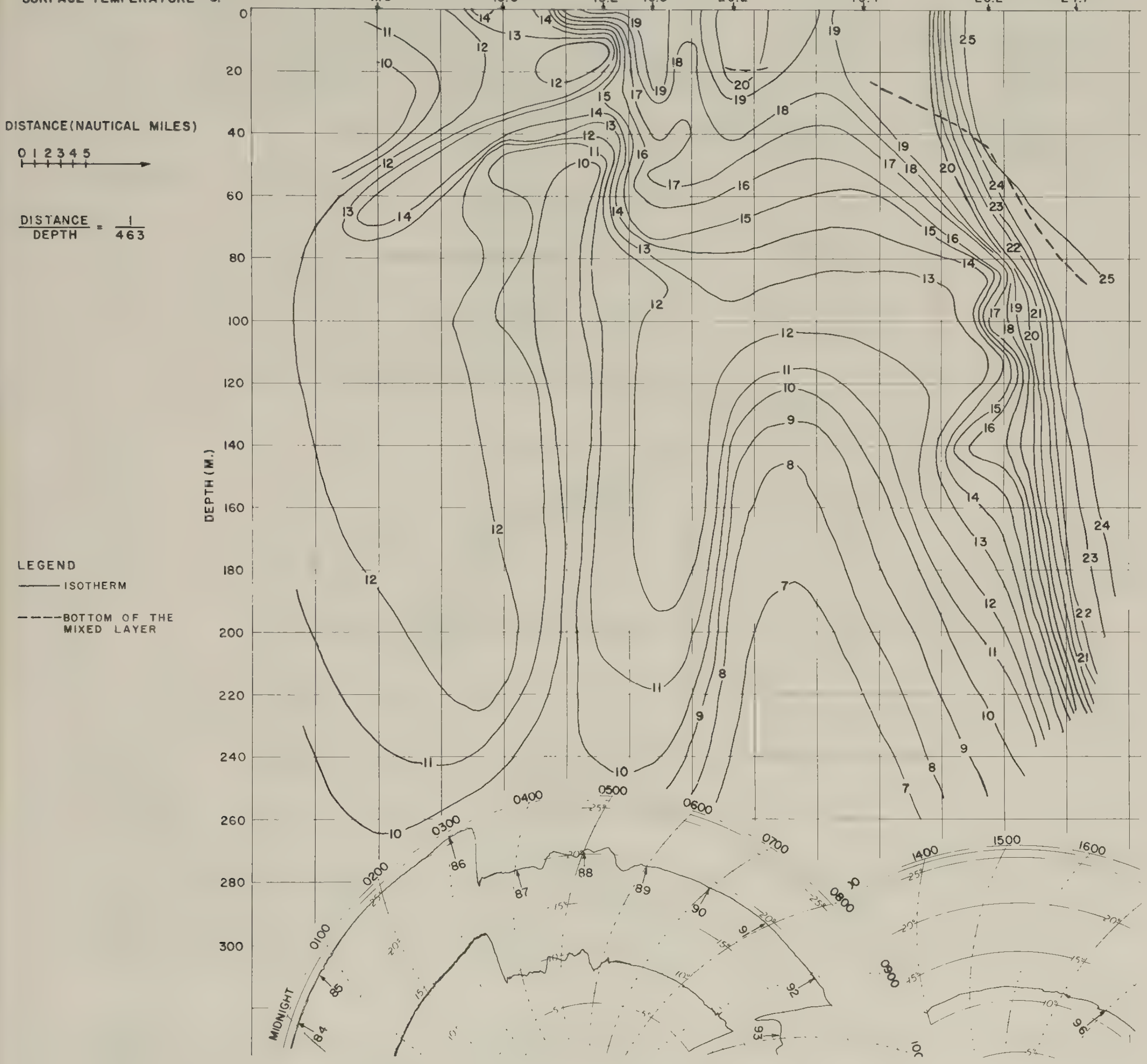


FIGURE 11.—Transect I—Section 9, May 16, 1963. (*See* caption for fig. 3.)

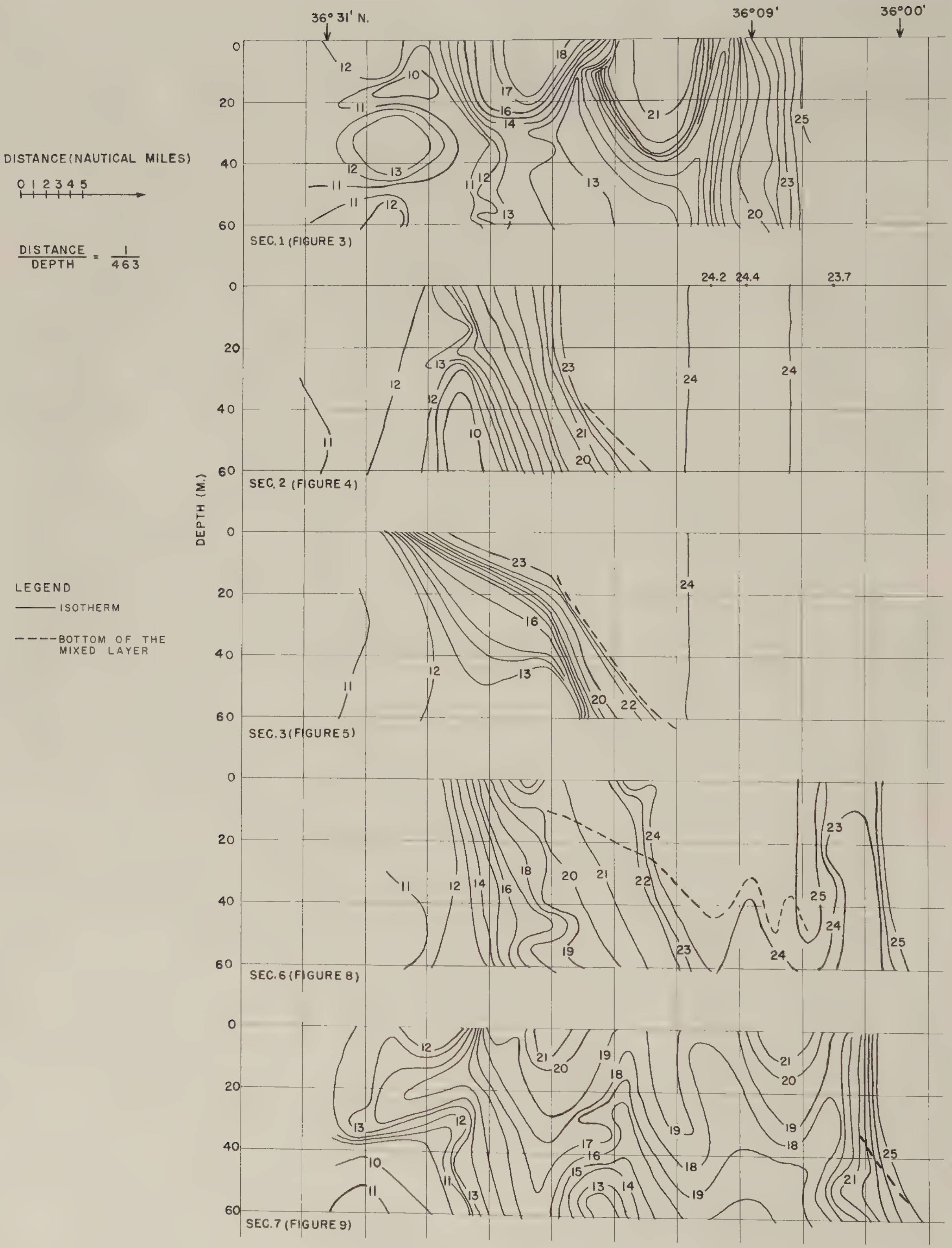


Figure 12.—Sections 1, 2, 3, 6, and 7 of transect I, surface to 60 m., replotted with corresponding geographical points in approximate vertical alignment.

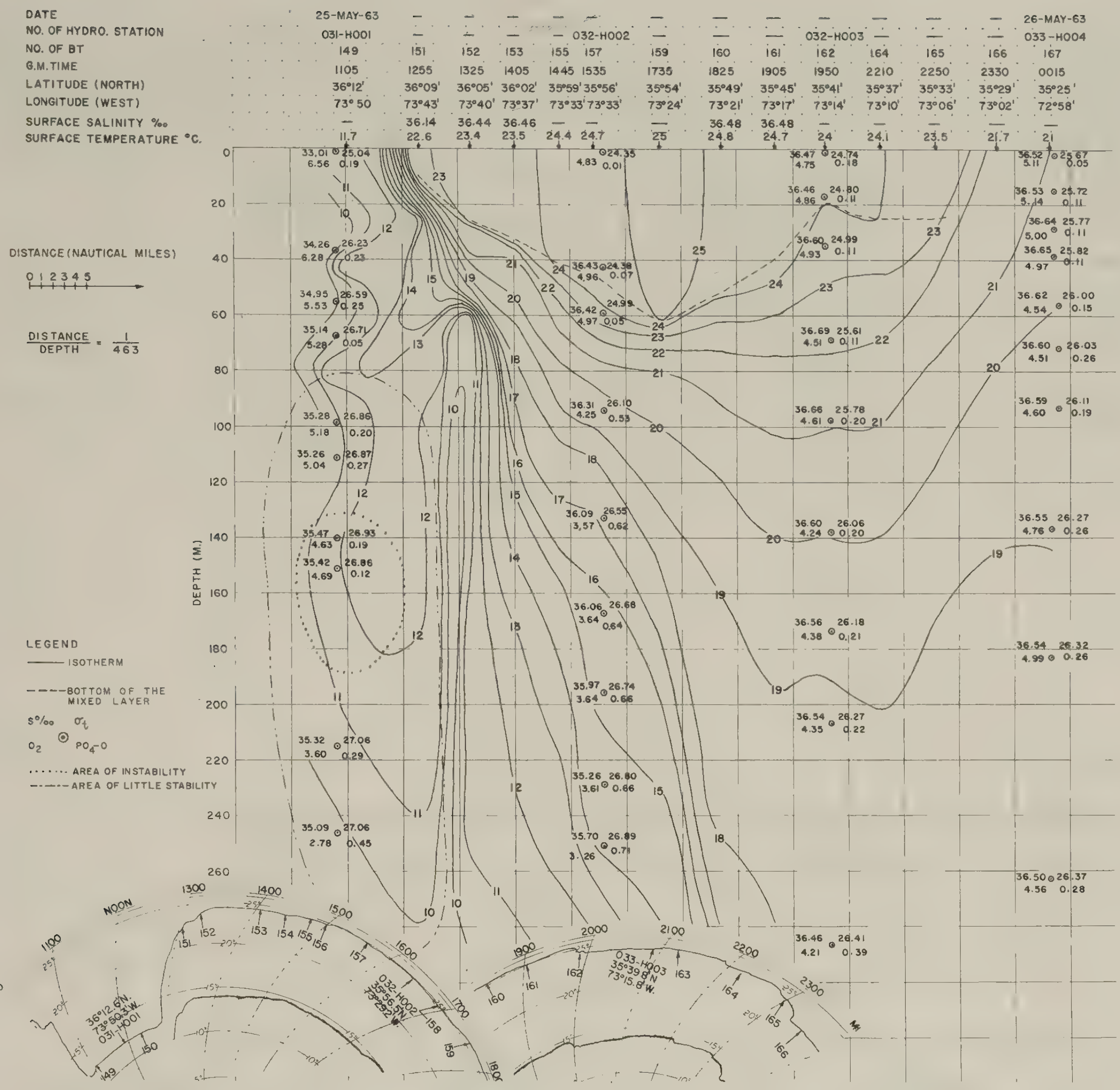


FIGURE 13.—Transect I—Section 10, May 25, 1963. Vertical temperature profile and thermograph record of surface temperatures. Thermograph temperatures greater than 25° C. are read from the lower of the two traces by adding 10° C. to the individual values. Bathythermogram numbers appear along the surface temperature trace to show the times of the casts. Data on salinity, density, dissolved oxygen (ml./l.), and inorganic phosphate (μg.-at./l.) are plotted on the vertical profile but not contoured.

the left boundary of the Gulf Stream in each transect is indicated in figure 1 by unbroken straight lines. The observed range of positions of the boundary on transects I and II is indicated by two parallel dashed lines. The mean and range of the boundary positions along transect I are based on observations during 14 crossings between May 10 and June 6, 1963, and along transect II on 5 consecutive crossings between May 31 and June 5, 1963. The range is not given along transect III because only three sections were made across the boundary (in 2 consecutive days).

Data are inadequate for the evaluation of horizontal movement of the left boundary or of the warm core between the transects. (Data from the only run along the boundary from transect II to transect I did not show significant meandering.) It is reasonable, nevertheless, to make inferences from transect I data,

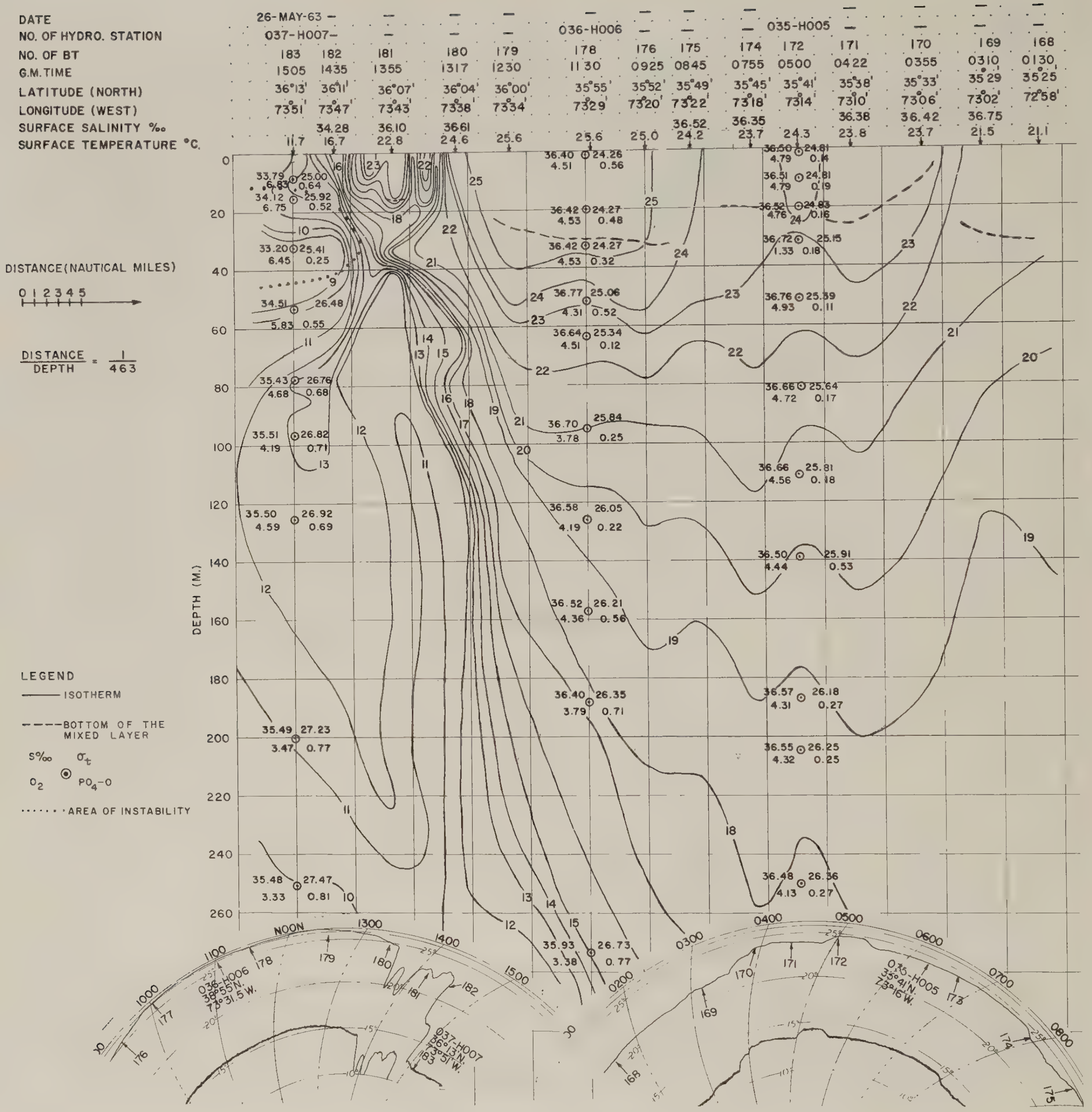


FIGURE 14.—Transect I—Section 11, May 26, 1963. (*See* caption for fig. 13.)

in which the position of the left side of the warm core oscillates by about 10 miles (18.5 km.) on either side of the mean (dotted line, fig. 1). The left boundary of the Gulf Stream was not more than 10 miles right of its mean position in any of the sections but was about twice as far left in one section.

The observations along transect I indicate that the oscillation of the left boundary of the Gulf Stream and the width of the intermediate zone were not directly interdependent. Formation of the intermediate zone did not necessarily depend on oscillation of the boundary—oscillation may presumably occur when the intermediate zone is nonexistent. Some boundary oscillations, however, did seem to be con-

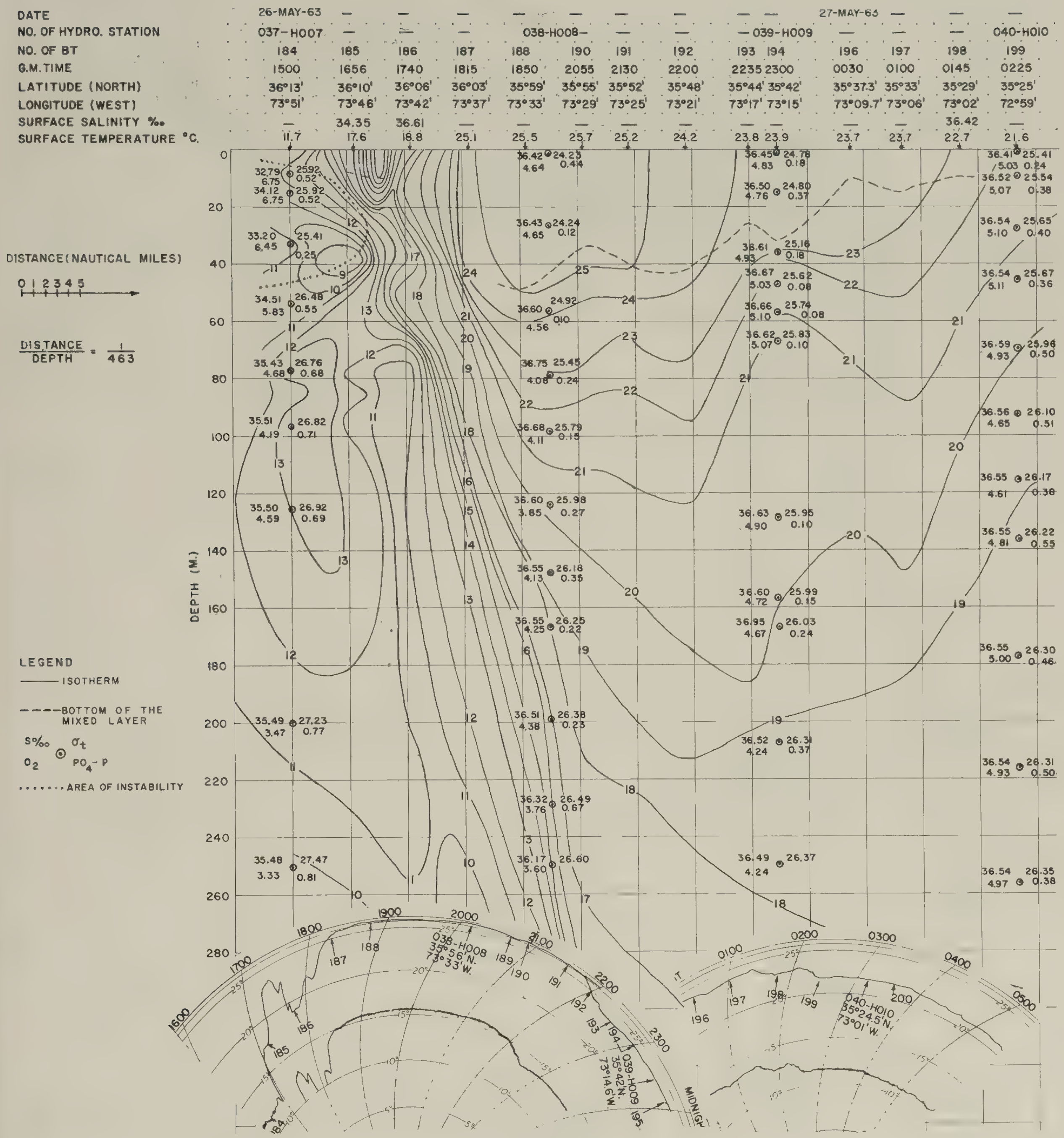


FIGURE 15.—Transect I—Section 12, May 26, 1963. (*See* caption for fig. 13.)

nected with development of an intermediate zone. The boundary during a well-developed intermediate zone was found right of its mean position, but the boundary during a weakly developed intermediate zone was left of its mean. Along transect II, the limited number of observations suggests that the pattern of oscillation was similar to that in transect I.

WARM CORE OF THE GULF STREAM

The core of warmest water was found at or near the left boundary of the Gulf Stream. The

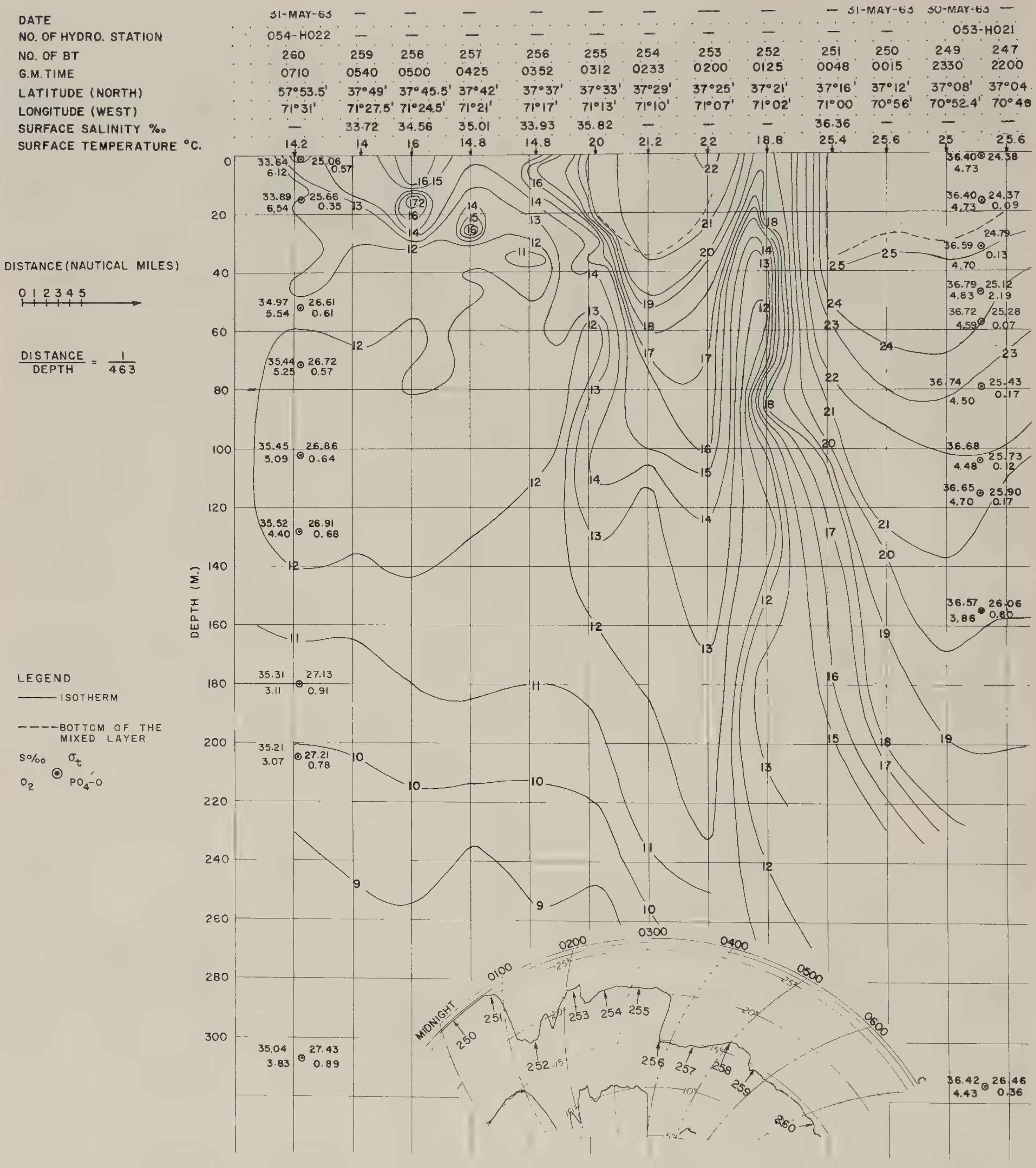


FIGURE 16.—Transect II—Section 13, May 31, 1963. (*See* caption for fig. 13.)

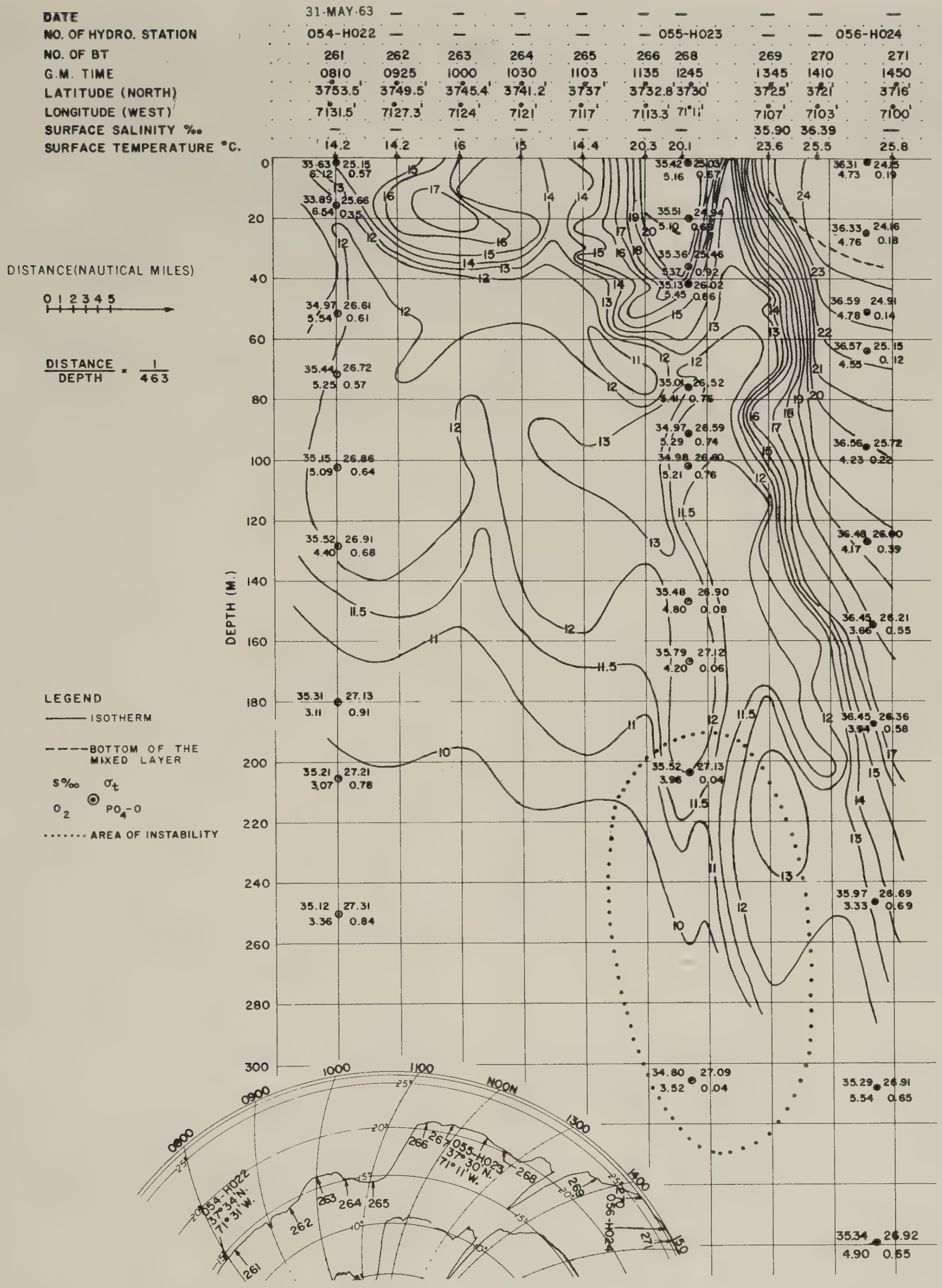
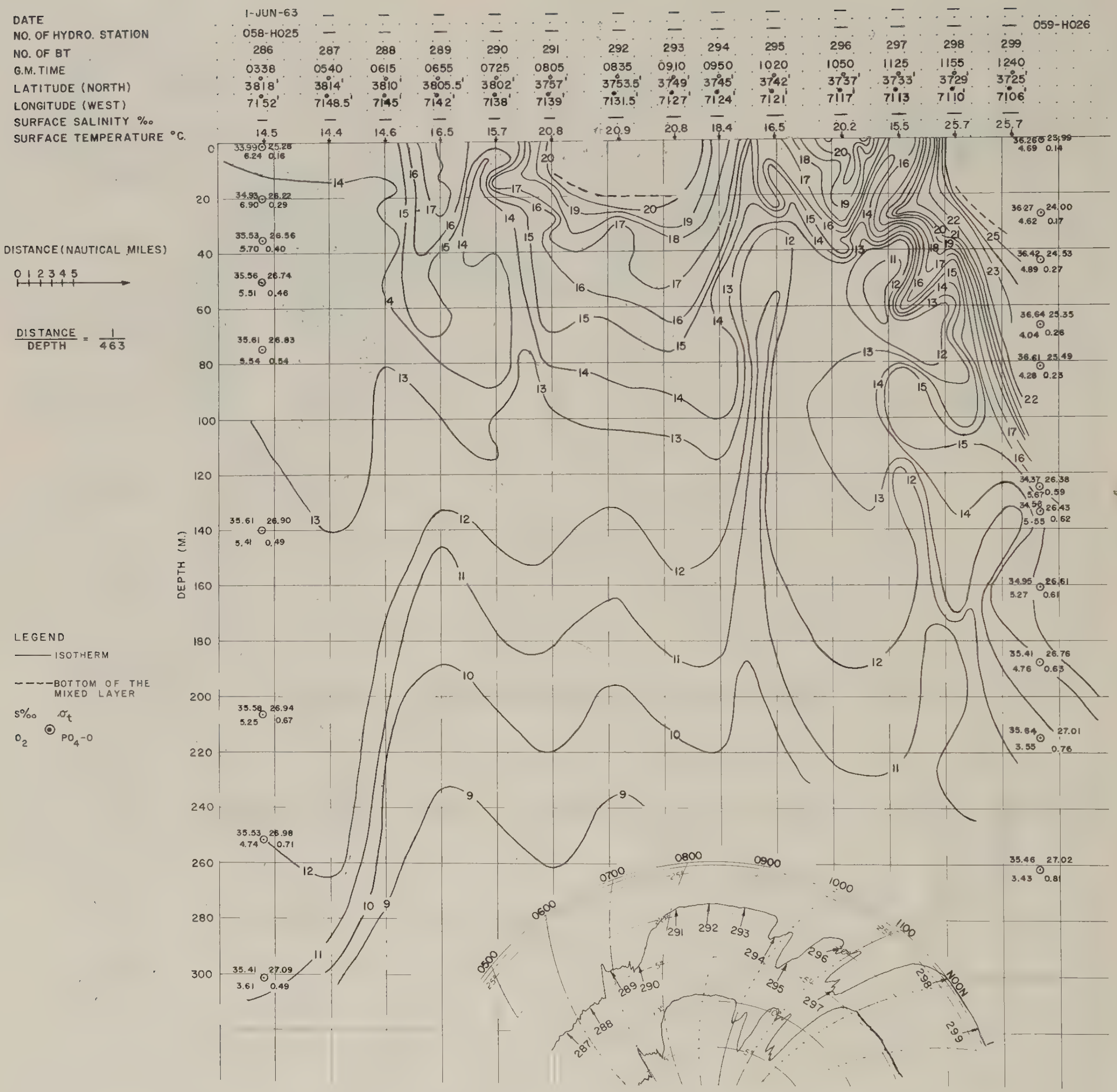


FIGURE 17.—Transect II—Section 14, May 31, 1963. (*See* caption for fig. 13.)



DATE	1-JUN-63	—	—	—	—	—	—	—	—	—	—	—	—	—
NO. OF HYDRO. STATION	058-H025	—	—	—	—	—	—	—	—	—	—	—	—	— 059-H026
NO. OF BT	286	287	288	289	290	291	292	293	294	295	296	297	298	299
G.M. TIME	0338	0540	0615	0655	0725	0805	0835	0910	0950	1020	1050	1125	1155	1240
LATITUDE (NORTH)	38°18'	38°14'	38°10'	38°05.5'	38°02'	37°57'	37°53.5'	37°49'	37°45'	37°42'	37°37'	37°33'	37°29'	37°25'
LONGITUDE (WEST)	71°52'	71°48.5'	71°45'	71°42'	71°38'	71°39'	71°31.5'	71°27'	71°24'	71°21'	71°17'	71°13	71°10'	71°06'
SURFACE SALINITY ‰	—	—	—	—	—	—	—	—	—	—	—	—	—	—
SURFACE TEMPERATURE °C.	14.5	14.4	14.6	16.5	15.7	20.8	20.9	20.8	18.4	16.5	20.2	15.5	25.7	25.7

DISTANCE (NAUTICAL MILES)
0 1 2 3 4 5
DISTANCE / DEPTH = 1 / 463
LEGEND
ISOTHERM
BOTTOM OF THE MIXED LAYER
S‰ σt
O2 PO4-O
DEPTH (M.)
0
20
40
60
80
100
120
140
160
180
200
220
240
260
280
300
33.99 25.28 6.24 0.16
34.93 26.22 6.90 0.29
35.53 26.56 5.70 0.40
35.56 26.74 5.51 0.46
35.61 26.83 5.54 0.54
35.61 26.90 5.41 0.49
35.58 26.94 5.25 0.67
35.53 26.98 4.74 0.71
35.41 27.09 3.61 0.49
36.26 23.99 4.69 0.14
36.27 24.00 4.62 0.17
36.42 24.53 4.89 0.27
36.64 25.35 4.04 0.26
36.61 25.49 4.28 0.23
34.37 26.38 5.67 0.59
34.56 26.43 5.55 0.62
34.95 26.61 5.27 0.61
35.41 26.76 4.76 0.63
35.64 27.01 3.55 0.76
35.46 27.02 3.43 0.81
0500
0600
0700
0800
0900
1000
1100
NOON

FIGURE 18.—Transect II—Section 15, June 1, 1963. (*See* caption for fig. 13.)

warm core is defined as that part of the Gulf Stream which was warmer than 24° C. in the period covered in this report.

RIGHT BOUNDARY OF THE GULF STREAM

The right boundary of the Gulf Stream is defined here as a strong horizontal temperature gradient at the surface as illustrated in figure 2 between BT's 367 and 366. The right boundary of the Stream was crossed three times along transect I. The mean position is indicated in figure 1 by a dash-dot line. Crossings were within a 2-day period, and the boundary was displaced slightly to the south on the third crossing. On the first crossing, the boundary appeared on the surface temperature record between BT's 165 and 166 (fig. 13); on the second crossing, between BT's 169 and 170 (fig.

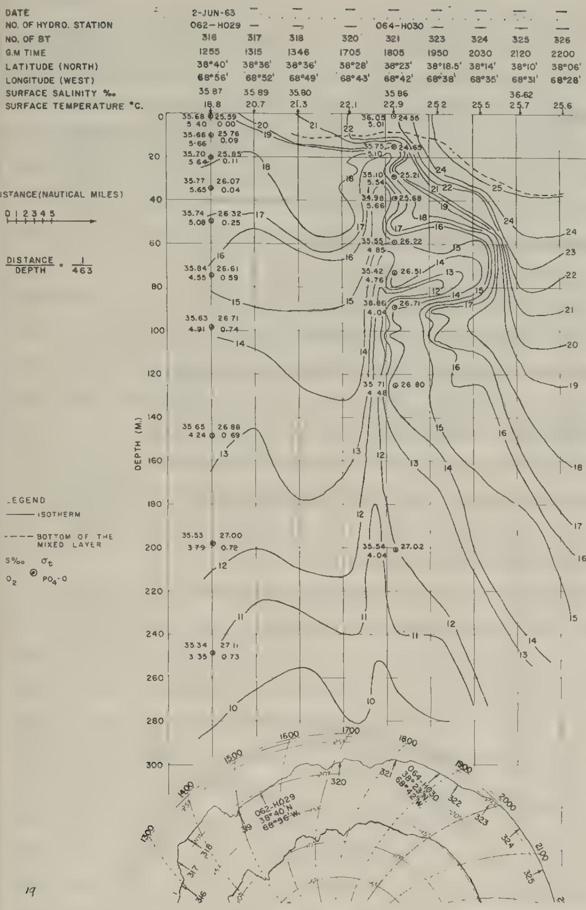


FIGURE 19.—Transect III—Section 16, June 2, 1963. (*See* caption for fig. 13.)

14); and on the third crossing, between BT's 197 and 199 (fig. 15).

The right boundary was crossed only once along transect II. Unfortunately, no surface temperatures are available because the recorder was temporarily out of order. Since the temperature difference between the Sargasso Sea and the Gulf Stream was 4° C., the boundary may have been even more distinct than along transect I.

The right boundary was crossed only once along transect III also; the crossing is shown on the surface temperature record between BT's 358 and 359 (fig. 21). The isolated peak on the trace represents an occasion when the ship was steered back and forth quickly across the boundary along legs about 200 m. long. At this time, the boundary was distinctly indicated by surface conditions. The sea was choppy on the Gulf Stream side but relatively smooth on the Sargasso Sea side, with no zone of transition—just a sharp line.

The right boundary was crossed again at lat. 37°12′ N. and long. 69°23′ W., while the vessel traveled from transect III to transect II (fig. 1; also see surface temperature trace in fig. 2). The boundary was crossed within 5 miles (9.3 km.). Since we were running obliquely to the Stream, the actual gradient at the boundary must have been considerably steeper than indicated on the trace.

The presence of a distinct right boundary on all occasions contradicts statements in the literature on the subject, to the effect that no detectable boundary exists between the Gulf Stream and the Sargasso Sea (Iselin, 1936, 1940). Possibly, of course, the boundary is not marked in the warm season, when the temperature of the surface waters is higher in the Sargasso Sea than in the Gulf Stream. Perhaps the right boundary is more typical of conditions in winter and spring than in other seasons.

WIDTH OF THE GULF STREAM

The Gulf Stream was about 50 miles (92.6 km.) wide along transects I and II, but about 70 miles (129.6 km.) along transect III. The greater width along transect III may not have represented a greater actual width of the Gulf Stream, but only a transient deformation of its right side. A similar deformation is indicated for the same day at this location in the U.S. Naval Oceanographic Office sea-surface temperature chart.

ENVIRONMENT OF THE GULF STREAM

The Gulf Stream structure, at the surface bounded on the left and right as defined in the previous section, consisted of a warm core flanked by rather small horizontal temperature gradients of varying widths. The warm core extended to depths of 60 to 80 m. over a width of 25 to 35 miles (46.3–64.8 km.). Mean values are given to facilitate comparison of the surface properties of the slope water, the Gulf Stream as a whole, the warm core of the Gulf Stream, and the Sargasso Sea (table 1). The slope water values are from five stations along transects I and II. None of these five stations was entirely out of Gulf Stream influence; therefore, the values are not entirely representative of typical slope water.

TABLE 1.—*Mean values of surface properties in the Gulf Stream and adjacent water masses (Geronimo Cruise 1)*

	Temperature	Salinity	σt	Oxygen	PO_4–P
	° *C.*	$^{\circ}/_{oo}$		*ml./l.*	*μg. at./l.*
Slope water	12.98	33.59	25.34	6.31	0.35
Gulf Stream (all stations)	25.01	36.42	24.41	4.76	.18
Gulf Stream (warm core stations only)	25.61	36.36	24.20	4.66	.27
Sargasso Sea	21.64	36.57	25.49	5.08	.15

The water masses of the slope water, Gulf Stream, and Sargasso Sea were distinctly different in all properties, both at the surface and in the subsurface layers. The subsurface properties left of the Gulf Stream were characteristically erratic; in the Gulf Stream and Sargasso Sea the properties tended to be regular, except for phosphate, which varied greatly to about 300 m.

INTERACTION OF THE SLOPE WATER AND THE GULF STREAM

The present data draw special attention to the transient nature of the intermediate zone at the left side of the Gulf Stream. In the first section with oceanographic stations (transect I, fig. 13), one sharp boundary appears where the surface temperature increased from 13° to 22° C. in about 2.5 miles (4.6 km.); the intermediate zone was almost nonexistent at the surface. In the transect of 24 hours later (fig. 14), the situation has changed drastically: the intermediate zone extends over 15 miles (27.8 km.), and two surface temperature boundaries are distinct. The variability of the width of the intermediate zone and its intermittent disappearance tend to demonstrate that its existence was the result of interaction between two water masses.

INTERACTION SYSTEMS

The intermediate zone has, of course, a vertical dimension. In the following interpretation, therefore, it is convenient to use the term "interaction system" for the entire volume of intermediate water.

The dimensions, shape, and internal structure of the interaction system shown in figures 3 and 4 change and transform rapidly, but the formation of the system seems to have a certain repetitive pattern. In figure 3 the intermediate zone is well developed. The two boundaries, enclosing the intermediate zone, are clearly marked on the surface temperature record. Temperature increases sharply by 7° C. at the slope water boundary, between the BT numbers 4 and 5. The intermediate zone is composed of two cold-water belts and two shallow warm-water cores. At the boundary between the intermediate zone and the Gulf Stream the temperature rises in two steps from about 15° in the cold belt to 24° in the Gulf Stream. A complicated pattern of the interaction extends in this section to about 230 m.

When the next section (fig. 4) was taken 2 days later, the boundary structure had changed. The intermediate zone with shallow currents and cold-water bands disappeared. Only one boundary was at the surface between the slope water (temperature 11.6° C. and salinity 33.75$^{0}/_{00}$) and the Gulf Stream (temperature 23.2° C. and salinity 36.29$^{0}/_{00}$); within the warm core the temperature was 24.2° C. and salinity 36.41$^{0}/_{00}$. Some traces in the interaction system can be observed in the subsurface. The surface temperature trace is relatively smooth along the steep temperature gradient in the boundary zone.

In the following section (fig. 5) the boundary was crossed about 6 hours later. The boundary zone is narrower than in the previous section. The temperature changes from 11.8° C. to 23° C. in about 4 miles (7.4 km.), and the surface temperature trace rises almost vertically, but, in general, the boundary structure does not change between the two sections. A large mass of 12° C. water is enclosed by cooler water in the subsurface.

The section in figure 6 shows the boundary about 5 hours later. The surface temperature trace shows a small disturbance within the boundary. The disturbance was not present in the previous section. In the subsurface the 12° C. water has been reduced in volume and has separated. A bubble of 13° C. water is at 45 m., but it is not certain whether it has been ad-

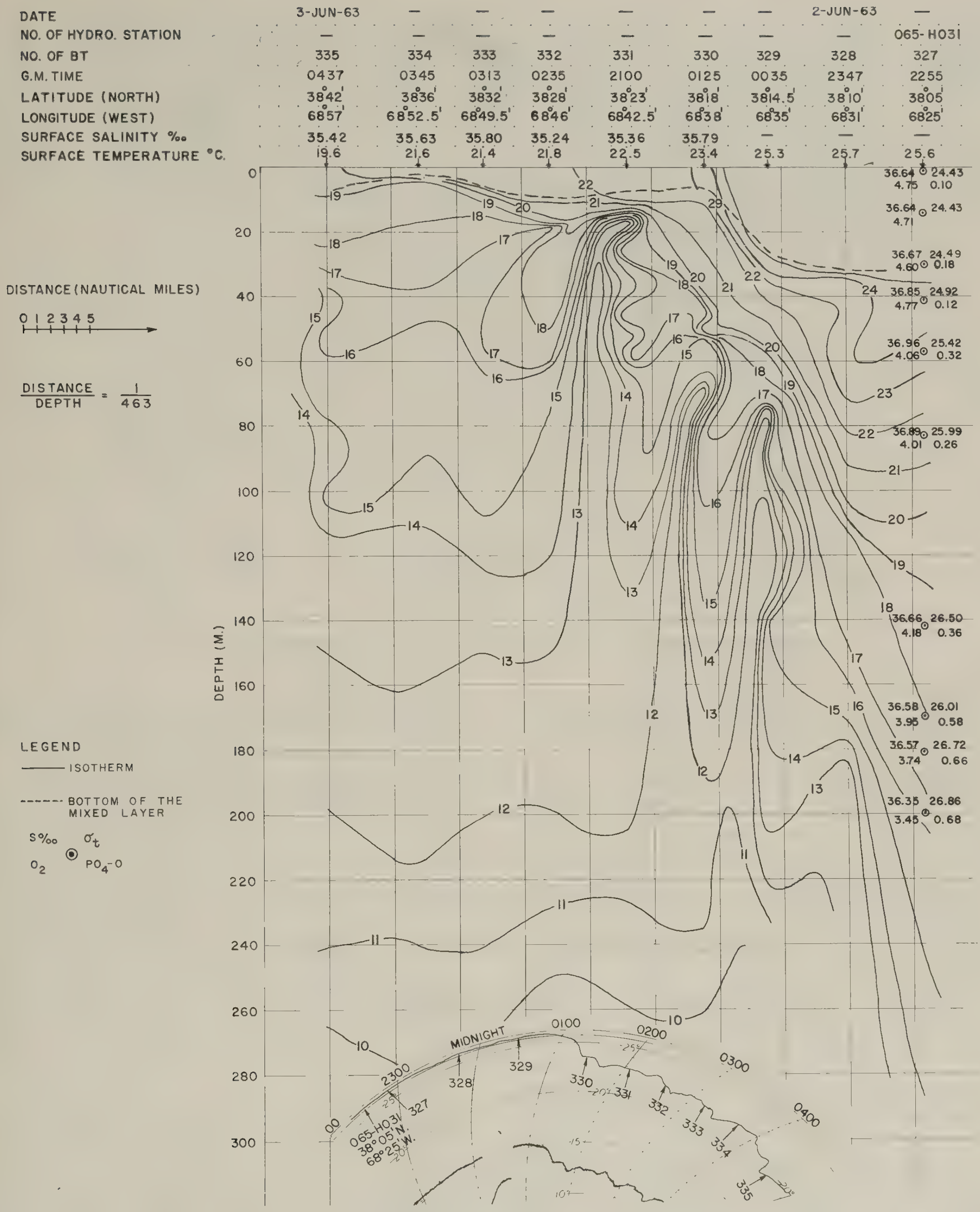


FIGURE 20.—Transect III—Section 17, June 3, 1963. (*See* caption for fig. 13.)

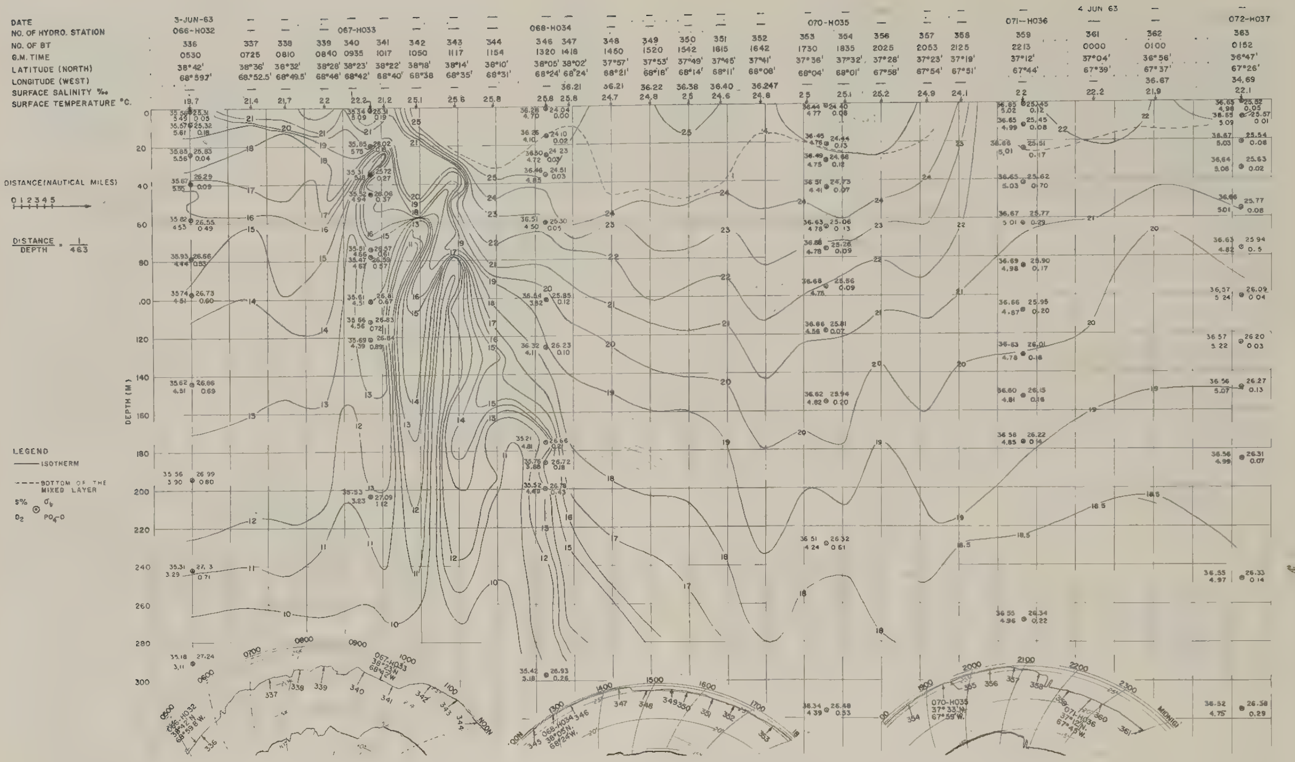


FIGURE 21.—Transect III—Section 18, June 3, 1963. (*See* caption for fig. 13.)

vected along the boundary or formed locally by occlusion of a lateral tongue of warmer boundary water.

About 7 hours later was the next crossing of the boundary (fig. 7). The boundary disturbance, which had just started in the previous section, had intensified and looked like a shallow small-scale upwelling with a cool belt very close to the Gulf Stream water. The surface temperature trace shows it as a cool-water stripe. The mass of 12° C. water in the subsurface has reduced further in volume. The warm bubble is at a shallower depth in this section than in the previous and is somewhat warmer. It may be either a new feature or a slow drifting of the same occluded warm water along the boundary. We could expect such an elongated bubble to be warmer in the center.

In the following section (fig. 8) about 5 hours later, a very large–scale process begins within the left side of the Gulf Stream. The former boundary is at about the same location, and the small-scale disturbance is still clearly marked on the surface temperature trace. A new boundary is forming 25 miles (46.3 km.) within the Gulf Stream near the velocity maximum. The cool belt at the surface is shown at the right section of the temperature record at BT number 65. The surface salinity in the cool stripe is 36.04 $^0/_{00}$ and, probably, is somewhat lower in its center. To the left and to the right of the cool band the surface salinities are 36.37 $^0/_{00}$ and 36.37 $^0/_{00}$. The bottom of the mixed layer is indicated by the dashed line. The cool band has no mixed layer. Apparently an intense upwelling process has been just started and is cutting off a very large portion of the Gulf Stream water from the main body of the Stream.

The next section shown in figure 9 was made about 20 hours later. The intermediate zone is about 35 miles (64.8 km.) wide and is at about the same stage of development as it was in the first section (fig. 3). The separated mass at the Gulf Stream is split into two shallow warm-water cores. The subsurface has changing jets or tongues of cold and warm water immediately

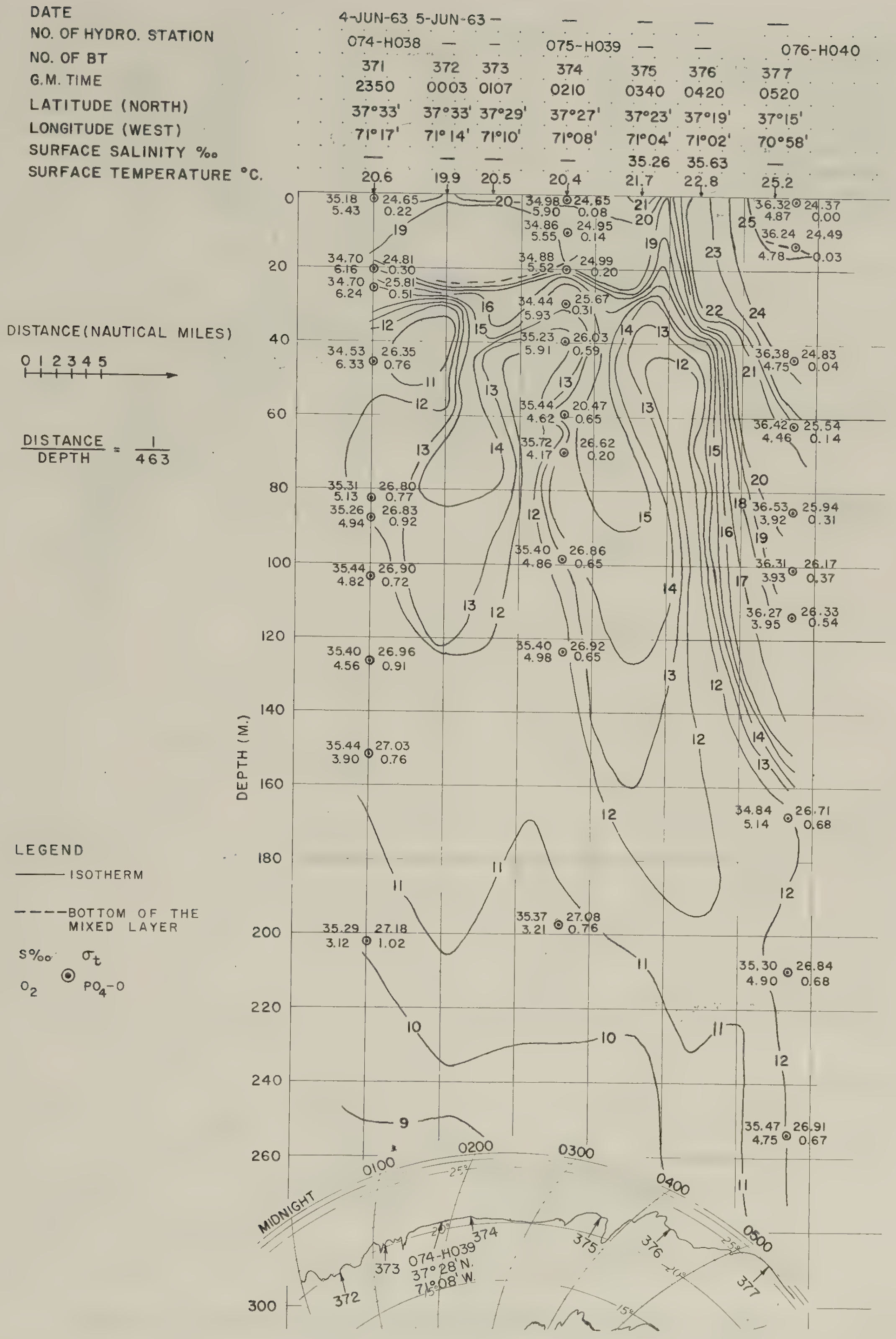


FIGURE 22.—Transect II—Section 19, June 4, 1963. (*See* caption for fig. 13.)

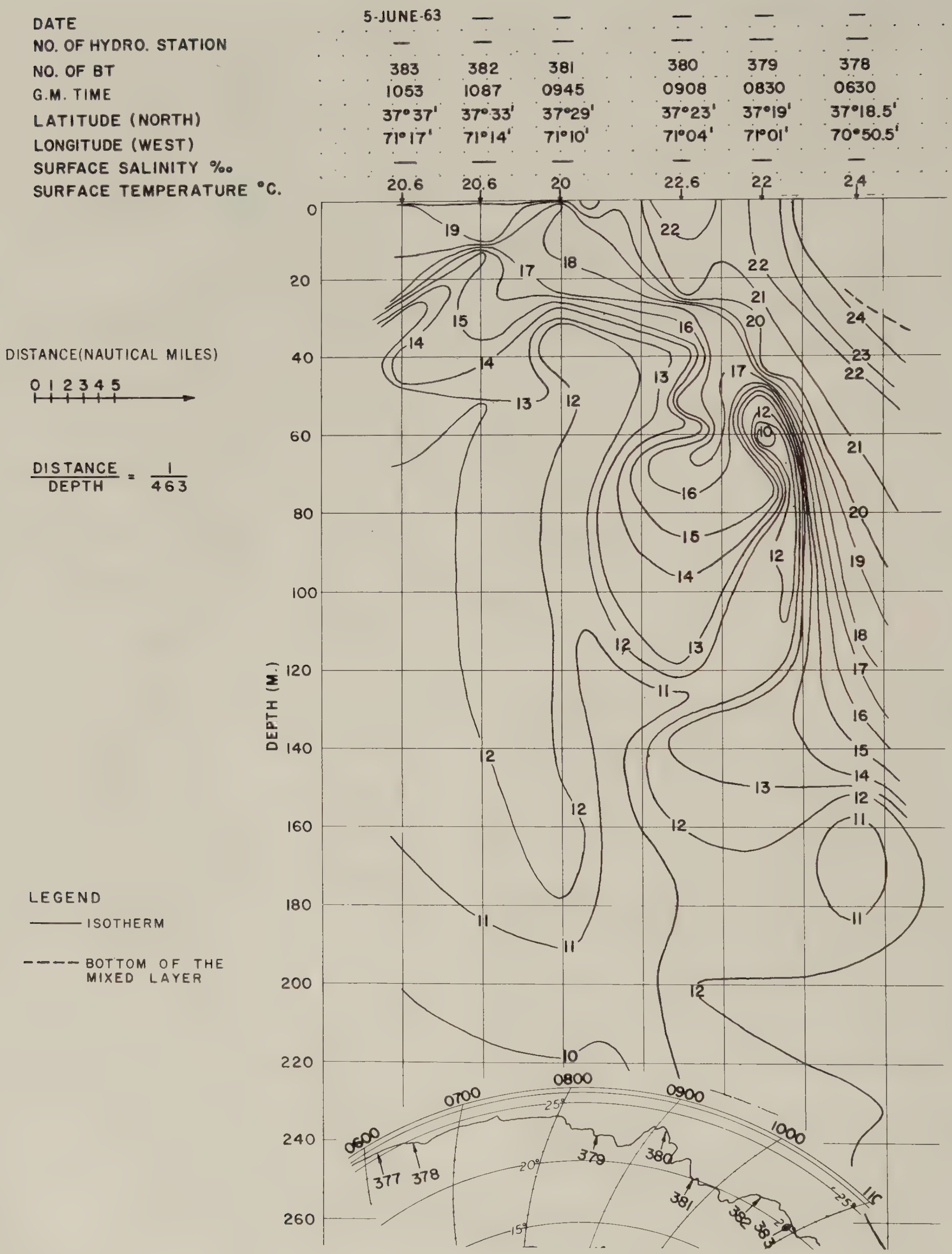


FIGURE 23.—Transect II—Section 20, June 5, 1963. (*See* caption for fig. 13.)

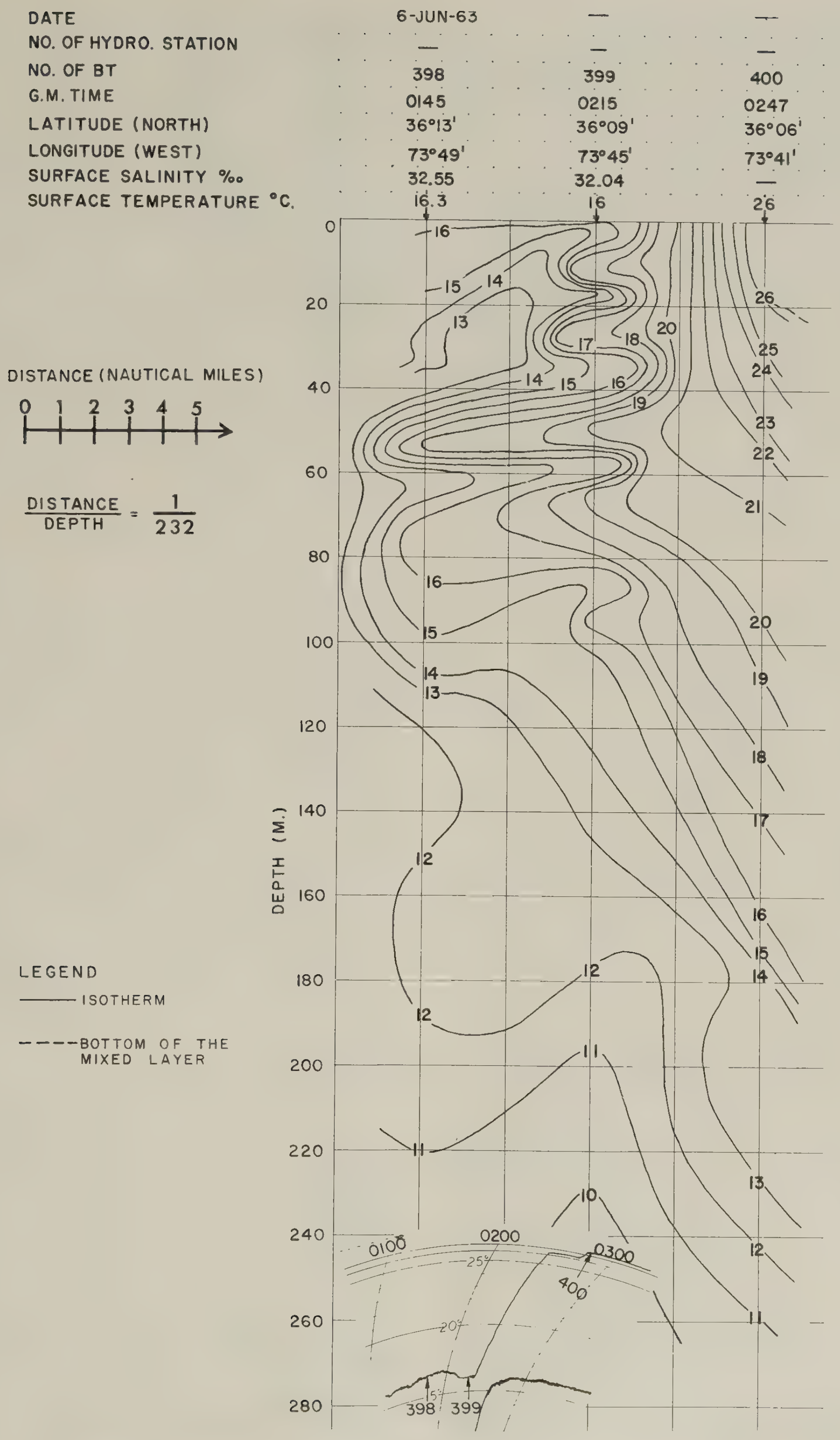


FIGURE 24.—Transect I—Section 21, June 6, 1963. (*See* caption for fig. 13.)

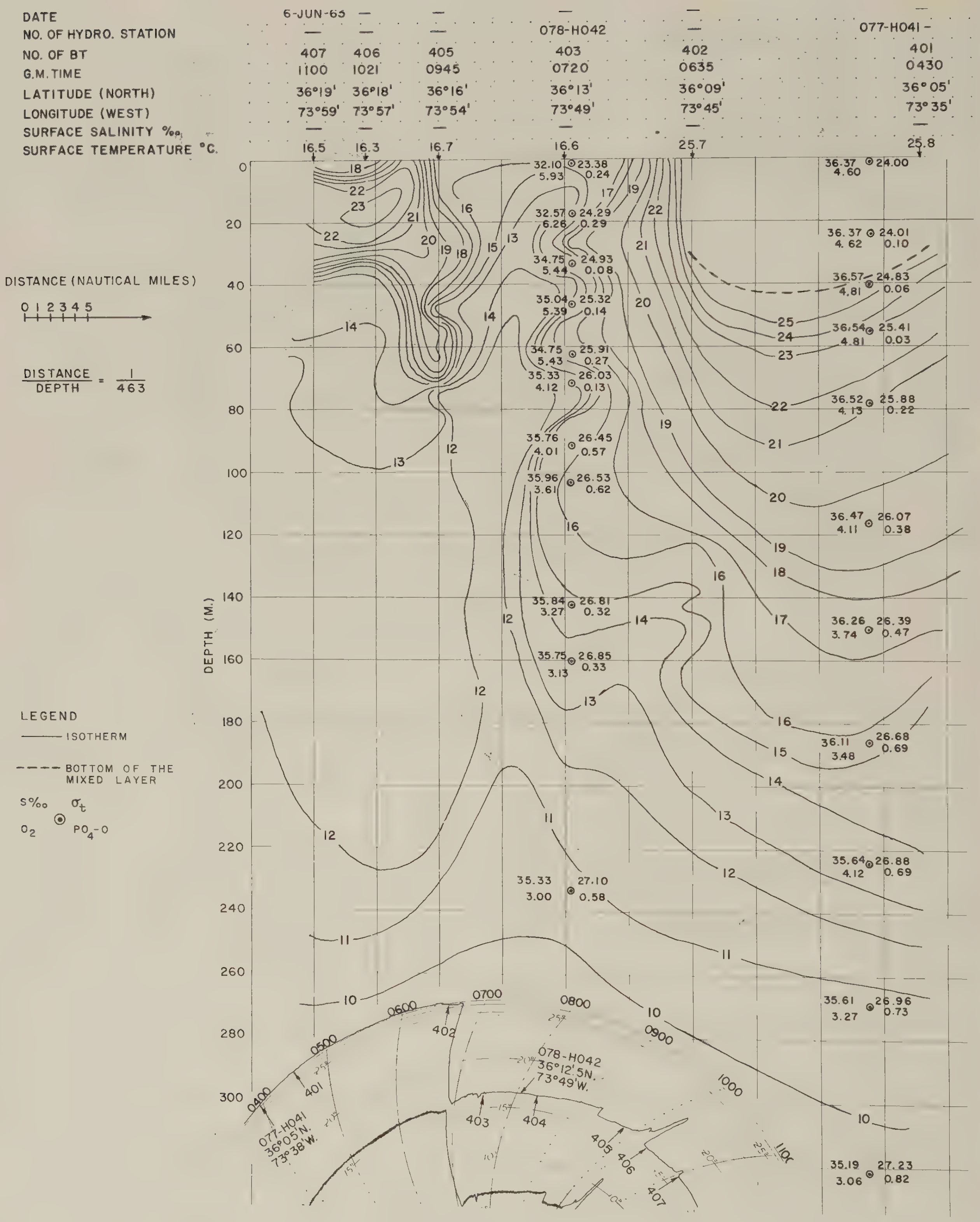


FIGURE 25.—Transect I—Section 22, June 6, 1963. (*See* caption for fig. 13.)

to the left of the slope water boundary at the surface.

The section shown in figure 10 was taken about 5 hours later, and one more section of the sequence was made 20 hours later (fig. 11). Both sections represent a dissipation stage of the interaction system which has been formed by the process shown in figure 8.

The thermal structure in figure 10 is somewhat simpler than in the previous section (fig. 9), but the two cold-water stripes, one near the Gulf Stream boundary and the other between the two shallow warm-water cores, are still very well marked on the surface temperature trace. The cold-water stripes are almost eliminated in the next section (fig. 11). The surface temperature is relatively smooth between the two steep temperature gradient zones at the boundaries on both sides of the intermediate zone.

A number of the sections indicate that the Gulf Stream boundary moved to the left during the absence of an interaction system. To illustrate this movement, the upper 60 m. of five of the sections from transect I were replotted (fig. 12), and corresponding geographic points were placed in approximate vertical alignment. (Full plots of these sections appear in figures 3, 4, 5, 8, and 9.) These sections start during one interaction cycle and end during the succeeding cycle, 4½ days later. Because the first and last of these sections represent about the same stage in the successive cycles, the time of a cycle from one strong and well-developed interaction system to another was about 4½ days (108 hours).

When the intermediate system decayed, the Gulf Stream boundary moved to the left and just one boundary remained. It became the slope water boundary when the new Gulf Stream boundary developed near lat. 36° N. The slope water boundary is almost exactly at the same location as it was in the previous cycle (fig. 3), but the new Gulf Stream boundary is about 6 miles (11.1 km.) farther to southeast and the intermediate zone is wider.

The next section across the Gulf Stream, along transect I (fig. 13), was made 10 days later. Oceanographic stations and BT's were taken in this and all the following sections. There was no intermediate zone, and the left boundary of the Gulf Stream corresponds to the situation in section 3 (fig. 5); however, this time the single boundary is about 24 miles (44.4 km.) to the southeast. Time interval between sections 3 and 10 was about 278 hours. If two cycles occurred during this time, the average period would be 139 hours.

Over half the cycle of a small interaction system was also recorded in three sections on transect I (figs. 13, 14, and 15). These figures suggest that about half the cycle was completed in 30 hours. This timing is in reasonable agreement with the 108-hour period estimated above for the cycle of a larger interaction system. Presumably the time of a cycle may vary considerably. The life span of an interaction system probably depends less on volume and shape than on the energy it contains after the separation stage.

The sections along transect II (figs. 16, 17, and 18) show stages in the maximum development of another strong interaction system. The three sections record such a small part of a complete cycle, however, that the duration of that cycle cannot be estimated.

The appearance of a rather weak interaction system can be detected in the sections along transect III (figs. 19, 20, and 21).

Altogether, six different interaction systems were observed during the *Geronimo* cruise. The mean cross-sectional area of the Gulf Stream water occluded into them is estimated to have been 1.69×10^6 m.^{2}

DIRECTION AND VELOCITY OF FLOW

Beginning at the stage of development shown in figure 8, the interaction system is cut off from the body of the Gulf Stream and acts independently. It presumably flows in the same general direction as the Gulf Stream, but the cold stripe that separates the interaction system from the Gulf Stream may have some tendency toward an opposite flow. This tendency is probably only occasionally strong enough to overcome opposing flow from both sides, induced by the horizontal shearing stress. Vertically, the cold stripes and the whole interaction system sometimes seem to extend to depths greater than 300 m. but many sections indicate that the rapid change of properties occurs above 300 m. (figs. 3, 16, 17, 18, and 22).

The geostrophic velocity computed with reference to 600 m. between stations 054–HO22 and 055–HO23 (fig. 17) was 23 cm./sec. The velocity must be considerably greater in the warm-water core of the interaction system (between hydrographic station 055–HO23 and the location of BT number 266, for example). The mean geostrophic velocity, with reference to 600 m. between stations 054–HO22 and 056–HO24, was 60 cm./sec, and between stations 055–HO23 and 056–HO24, it was 128 cm./sec. Because station 056–HO24 was located in the warm core of the Gulf Stream, the data are not applicable to the evaluation of energy left in the interaction system. The 600-m. reference level may be satisfactory for stations 054–HO22 and 055–HO23 but not for station 056–HO24. Additionally, this station is on the Gulf Stream side of the cold stripe. The mean geostrophic velocity computed between stations 054–HO22 and 055–HO23 appears realistic. No great velocities within the interaction systems were observed from the *Geronimo*.

PROCESS OF INTERACTION

Apparently Gulf Stream water was supplied to the interaction systems in two principal ways. During the present observations, the dominant supply was furnished by separation. A large volume of water is separated from the left flank of the main body of the Gulf Stream —for example see figure 8.

A supplementary supply of water was by injection. Tongues of warm and cold water alternating vertically extended over a considerable horizontal distance (fig. 24). The injections tended to be moderate to weak when the main interaction system was strong (figs. 8 and 16); conversely, the injection tongues tended to be actively developed when the main interaction system was nearly dissipated (figs. 10 and 11). A general idea of the dimensions of the warm-water tongues can be obtained from a profile based on BT observations along the slope water of the left boundary of the Gulf Stream, between transects I and II (fig. 26). The figure, which covers a distance of 140 miles (259.3 km.), shows one well-developed, warm-water tongue and a few cold tongues. The well-developed tongues were about 30 miles (55.6 km.) wide (parallel to the Gulf Stream boundary) and about 40 m. thick (vertical dimension) near the base. Their average projection was about 8 miles (14.8 km.) in the direction normal to the boundary, as evaluated from 11 well-developed examples in various sections. Gulf Stream water was not a contributing factor to numerous other tongues that seemed to have developed within the interaction system after separation (figs. 9 and 10).

DEVELOPMENT AND DISSIPATION

Two principal questions may be asked regarding the interaction systems; How or why do they develop, and what happens to the water mass separated from the Gulf Stream? When an interaction system had dissipated at the surface—whatever its dimensions or character —there remained just one sharp surface boundary between the slope water and Gulf Stream (figs. 5 and 13). It seems, however, that in depths from about 40 to 200 m., the interaction systems persisted for longer periods; possibly they never decayed completely. The sequence shown in figures 4 through 8 reveals that the remnants of an old interaction system appear to be absorbed by a new one. If volumes of water as large as those involved in interaction systems are disposed of by absorption within the neighboring water masses, perceptible changes in the character of these masses could be expected. Yet in our repeated sections along transect I (in a 1-month period), even though several interaction systems developed and dissipated, no appreciable change of properties was observed in the adjacent Gulf Stream and slope water. A small rise in temperature in the slope water can be attributed to heating as the warming season progressed. Slope water was less distinctly uniform at transect II than at transect I, but because the observation period was comparatively brief, no definite conclusions can be reached about the persistence of properties.

The slope water was warmer—by about 2° to 3° C.—at transect III than at transect I. The multistream structure of the Gulf Stream as represented by Fuglister (1951) was probably absent at transect I, but may have been start-

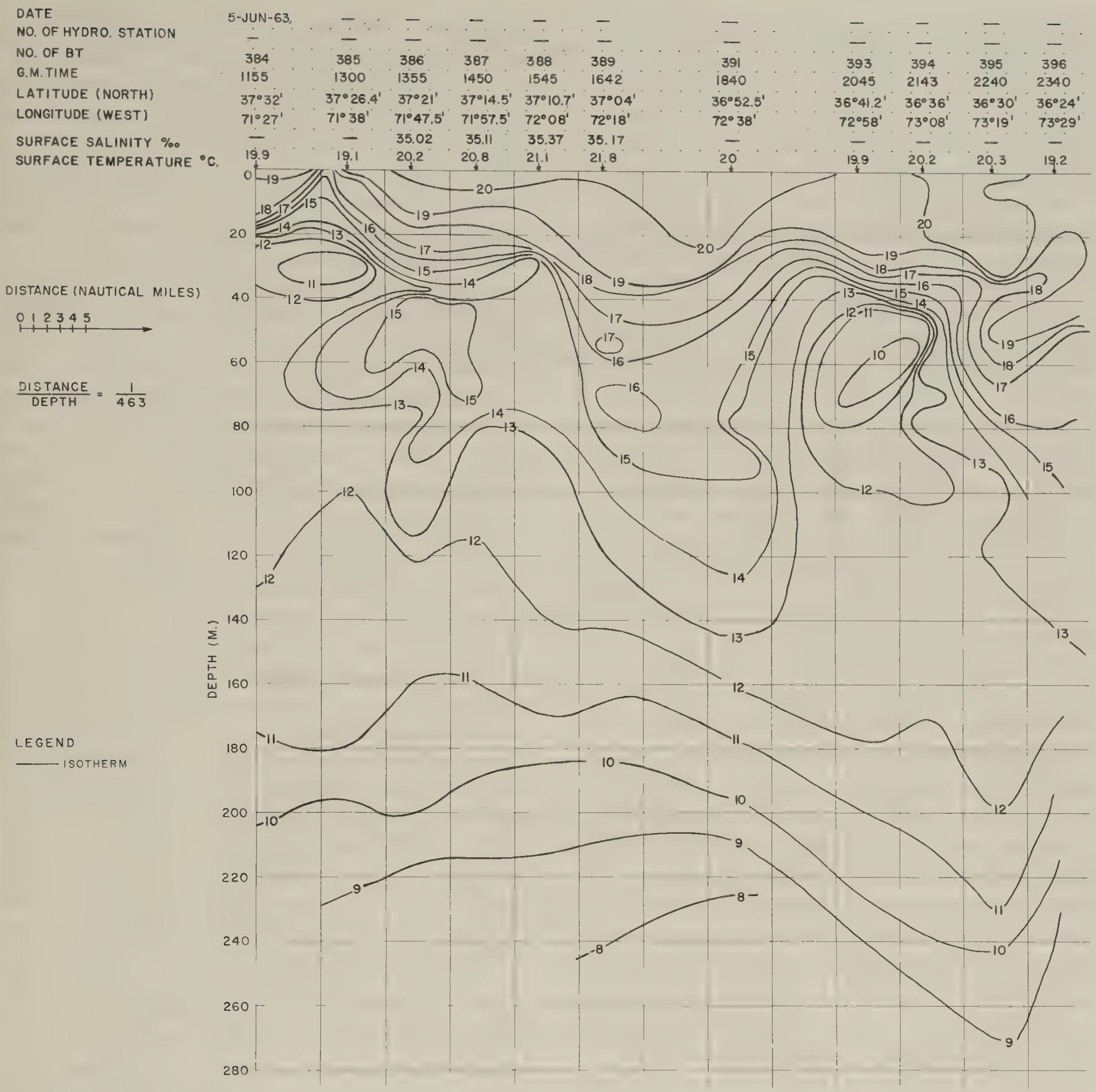


FIGURE 26.—Vertical temperature profile along the left boundary of the Gulf Stream between transects I and II.

ing to develop in the area between transects II and III. Thus, the likelihood exists that, in the process of dissipation, at least part of the mass of the interaction systems seen in the general area of transects I and II was channeled into secondary streams, and that these streams developed farther downstream into a multistream complex.

RETURN OF MIXED WATER TO THE GULF STREAM

A considerable part of the mass of a dissipating interaction system may be returned to the main body of the Gulf Stream at deeper levels than its point of origin. This assumption is supported by the fact that water properties in the interaction systems at depths of about

120 to 170 m. were generally the same as within the left side of the Gulf Stream at depths of 300 to 600 m. This similarity is illustrated in figures 27 to 30, which show temperature-salinity curves for the oceanographic stations made in sections 10, 12, 13, and 19. Coincidence of properties started at about $\sigma_t = 27.0$ and continued to the end of the curves (a little below 600 m.) where the approximate value is $\sigma_t = 27.8$. (The properties at 600 to 700 m. in the right side of the Gulf Stream and in the adjacent Sargasso Sea were entirely different—see the T–S curves of stations 051–HO19 and 052–HO20 in figure 27.)

The mean upper level of water with coinciding properties, computed from all available sections, was 355 m. for the left side of the Gulf Stream and 154 m. for the interaction systems. The horizontal distance between the generation area in the interaction systems and the locations of similar water in the Gulf Stream was 15 to 40 miles.

Most of the interchanging cold and warm tongues observed in the boundary area and in the interaction system were stable. When unstable situations do occur in the ocean, they are usually of short duration and it is difficult to obtain data on their frequency and the volumes. Unstable mass distributions may be created either by caballing or by rapid overflow of water of greater density over water of lesser density in the process of strong, lateral mixing. Oceanographic stations 031–HO01, 037–HO07, and 055–HO23 illustrate such unstable situations (figs. 13, 15, and 17). The instability, even if very limited in volume, was evident in 3 out of the 10 stations for which salinity data were obtained in the intermediate zone, whereas the total number of oceanographic stations was 42. The proportions may indicate that volumes of water exhibiting unstable mass distribution frequently occurred but lasted for only a brief period. Certainly errors in the data have to be considered; however, the three cases of instability occurred in the zone of intense interaction and none was outside of that zone. This fact indicates that the unstable situations were probably real.

ZONES OF CONVERGENCE AND DIVERGENCE

The left side of an interaction system is a zone of convergence with a rather permanent downward motion. When an interaction system dissipates, the convergence zone may be expected to move close to the left side of the Gulf Stream boundary. Downward motion caused by convergence is probably locally limited and too weak to transfer significant mass from an interaction system to the Gulf Stream. A superimposed momentum due to transient unstable mass distribution may, however, produce a downward flow strong enough to cover the horizontal distance between the generating and the discharging areas. The descending dense water would be absorbed by the left side of the Gulf Stream at levels about 200 m. lower than its point of origin in the interaction system. The downward motion, in turn, would intensify the surface convergence and, thus, produce a significant cross-current velocity component in the left side of the Gulf Stream.

The mean distance from the left boundary of the Gulf Stream to the location of maximum velocity in the Gulf Stream was 22 miles (40.7 km.), derived from four sections of surface velocity distribution across the current (Von Arx, 1952; Worthington, 1954). The distance between the right boundary of the Stream and the location of maximum velocity was 36 miles (66.7 km.). Outcroppings of cool water were present about 25 miles (46.3 km.) from the left boundary of the Stream, as can be seen from sections 3 and 6 (fig. 12) or by comparing sections 4 and 5 (figs. 6 and 7) with sections 6 and 7 (figs. 8 and 9). Thus, the cold stripe probably developed in the region of maximum velocity in the Gulf Stream, above the right flank of the steeply sloping isotherms, about where the 18° C. isotherm crossed the 200–m. level in section 5 (fig. 7).

Because of a strong cyclonic shear at the left of a velocity maximum and a slightly weaker anticyclonic shear at its right, a maximum horizontal gradient of the vertical component of absolute vorticity may be expected in the region of maximum velocity. The strong horizontal change in absolute vorticity may cause a tendency to diverge. If convergence in the area of interaction were intensified through the

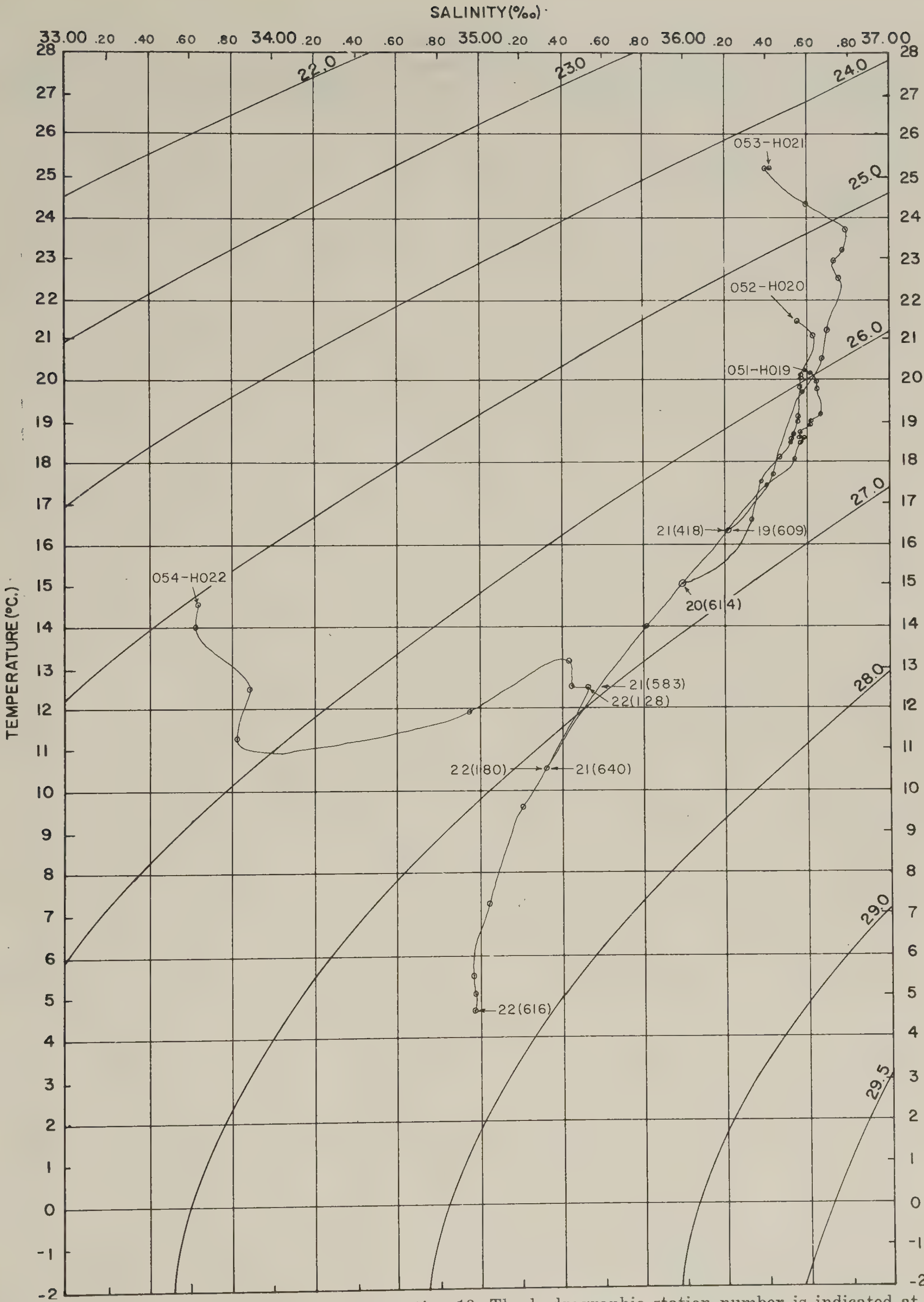


FIGURE 27.—Temperature–salinity curves along section 13. The hydrographic station number is indicated at the top of each trace. The last two digits of these station numbers also appear at points where the traces come close together or coincide. The depths of these points appear in parentheses.

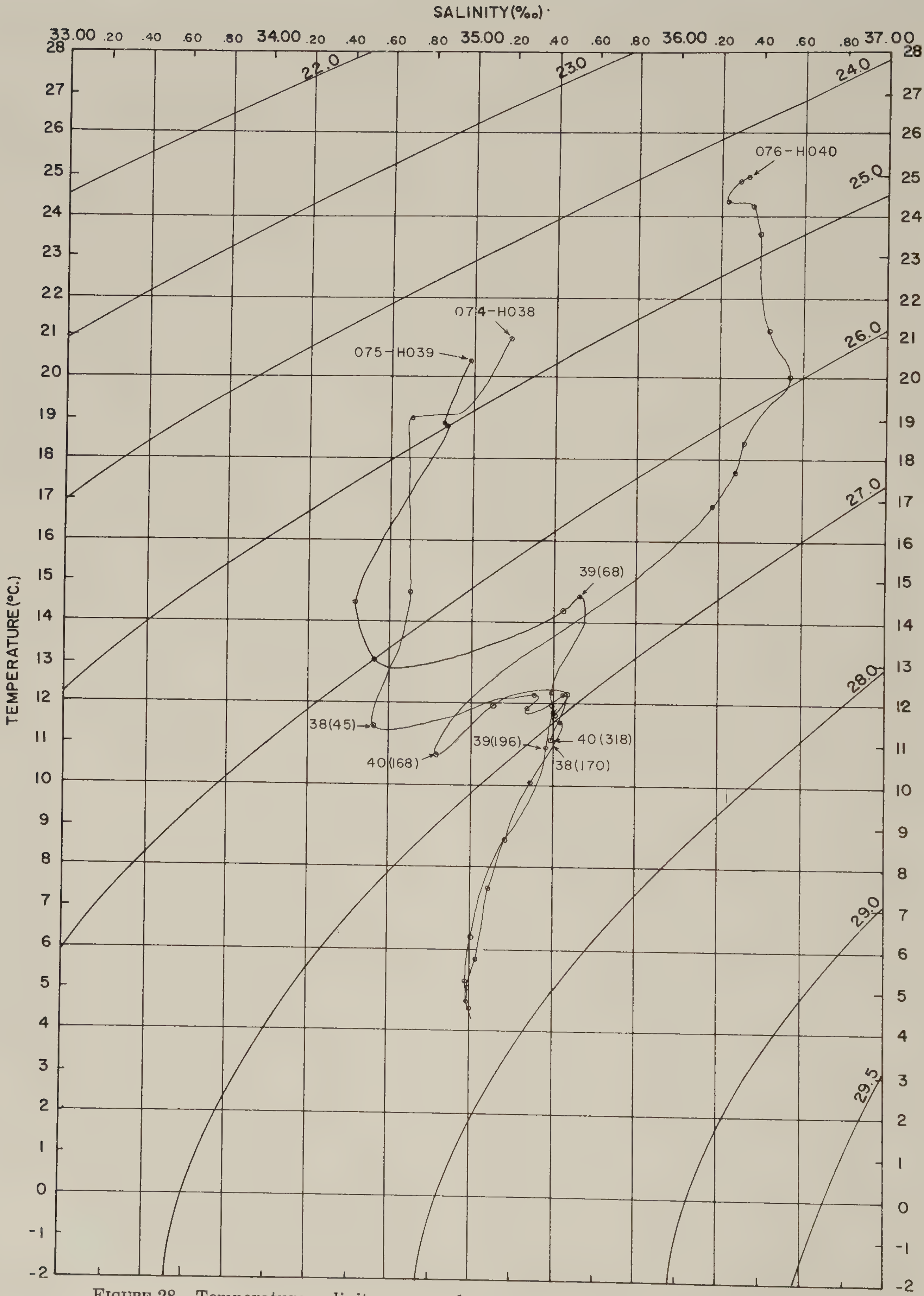


FIGURE 28.—Temperature–salinity curves along section 19. (*See* caption for fig. 27.)

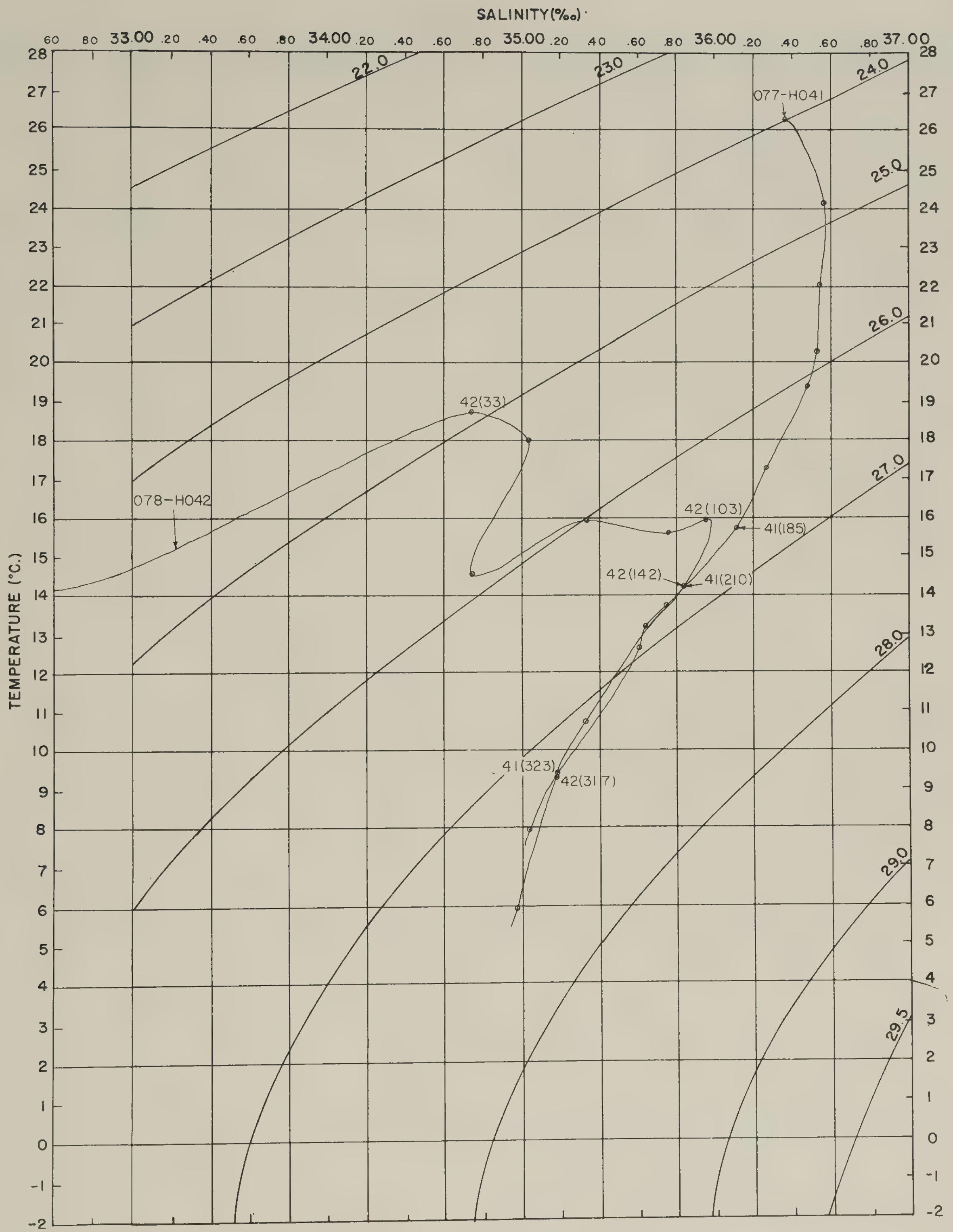


FIGURE 29.—Temperature–salinity curves along section 22. (*See* caption for fig. 27.)

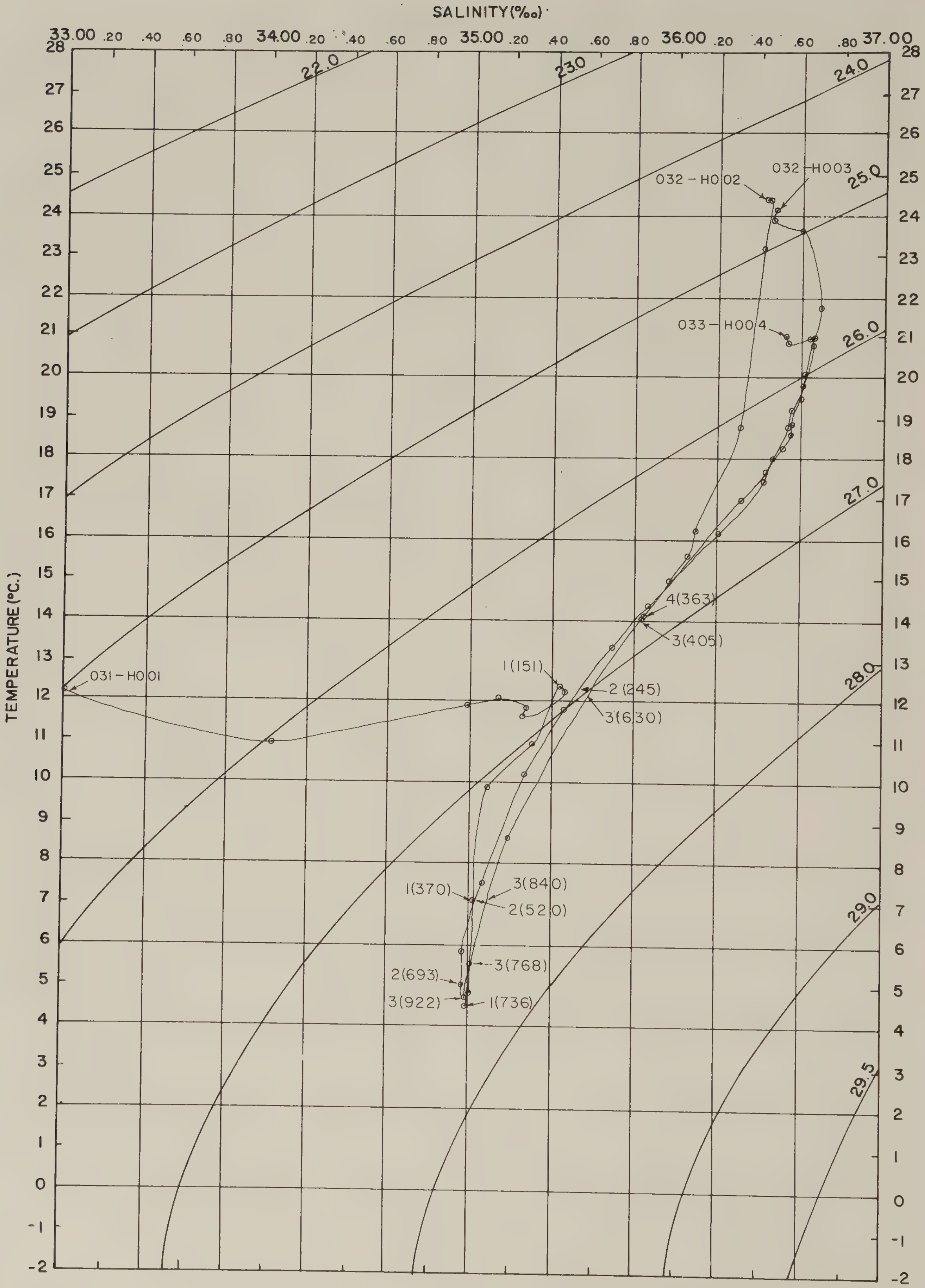


FIGURE 30.—Temperature-salinity curves along section 10. (*See* caption for fig. 27.)

mechanism of mixing during some phase of an interaction cycle, the cross-current component would be produced as a chain effect, and the tendency toward divergence might consequently result in an effective upwelling.

ORIGIN OF THE COLD STRIPES

The cold stripes at the left side of the Gulf Stream are of Shelf water origin, as shown by Ford, Longard, and Banks (1952). Their conclusions were based mainly on two sections (at about long. 55° and 57°) of "Operation Cabot" (1950), which extended over strongly meandering parts of the Gulf Stream. Stommel (1958), generalizing on their results, concluded that the influx of Shelf water must occur somewhere near Cape Hatteras, that the integrity of the cold stripe is maintained for 1,600 miles (2,963 km.), and that water exchange across the boundary is, therefore, negligible.

No such integrity of the cold stripe could be observed during the *Geronimo* cruise. Clear indications that local generation of cold stripes was caused by ascent of cool water may be seen in sections 4 to 7 (figs. 6 to 9). A rather simple boundary structure and no significant cold stripe appear in section 4 (fig. 6). About 12 hours later, when section 6 (fig. 8) was made, the boundary seen in figure 6 was at the same location, but a new boundary and cold stripe were developing strongly 25 miles to the right, far into the Gulf Stream.

The outcropping of cool water seems to have reached a maximum in section 7 (fig. 9). The old boundary is disintegrating below the surface, and the major zone of steeply sloping isotherms is located at the new boundary.

When interaction systems were fully developed and separated from the Gulf Stream by a cold stripe (figs. 10, 14, 16, 17, and 22), the presence of a well-developed mixed layer on both sides of (but not *in*) the stripe, indicated a strong ascending process. Furthermore, the temperatures and salinities of the cold stripes were similar to those in deeper water. For example, the surface temperature in the cold stripe in figure 9 (section 7) is 18° C. No surface salinity values are available for this part of the section, but the previous section (fig. 8) shows a surface salinity of 36.04 ‰ in the newly forming cold stripe (BT 65), while considerably higher surface salinities occur on either side. Salinities and temperatures similar to those found at the surface in the cold stripe in sections 6 and 7 (figs. 8 and 9) were found at a depth of about 160 m. in section 10 at oceanographic station 032–HO02 (fig. 13)—about 20 miles right of the boundary where the isotherms slope steeply. A similar example is provided by the surface conditions at the BT number 269 in figure 17. In figure 22, the surface salinity near the cold stripe (BT 375) is similar to the salinity of the Gulf Stream at 210 m. (station 076–HO40). The hypothesis that the cold stripes were caused by upwelling of water from the area of steeply sloping isotherms seems to be in agreement with the positions of the frontal outcrop as observed from an airplane (Von Arx, Bumpus, and Richardson, 1955). As previously pointed out, a supply of cold, low-salinity water by injection (cold tongues) was also observed during the *Geronimo* cruise. In some portions of the Gulf Stream, this source of cold water to the left of the Gulf Stream may be predominant.

PHOSPHATE DISTRIBUTION

In general, phosphate values were considerably higher in the surface waters of the interaction systems than in the Gulf Stream. Also, phosphate values fluctuated in the interaction systems, associated with interchanging tongues of cold and warm water, and the observed cold-water masses usually showed higher phosphate values. The higher phosphate content of interaction systems could come from various sources, including—although the evidence is sparse— the ascending water. To illustrate this assumption, the only oceanographic station close enough to the cold stripe to be indicative (station 055–HO23 in fig. 17) shows high phosphate values from the surface to about 130 m., low values from about 130 to 300 m., and high values again below 300 m. It seems that at this particular station, ascending water was present above 130 m., and descending mixed water (exhausted of phosphate) between 130 and 300 m. At station 056–HO24 (fig. 17) the phosphate content of the 15° C. water along the steeply sloping isotherms at about 220 m. was about the same. Water in the cold stripe was evidently ascending obliquely at this station, following the sloping density surfaces like Neumann's (1952) "gliding Austausch."

MIXING VOLUMES

According to the described process, Gulf Stream water moves through the interaction system from the surface layer to deeper levels after attaining higher density through mixing. This hypothesis requires mixing of a substantial amount of slope water into the returning mass. Along transect I, the ratio of Gulf Stream water to slope water in the mixture was obtained by applying salinities to the mixing equation, $S(M_1+M_2)=M_1S_1+M_2S_2$ where: M_1 is the mass in the slope water that corresponds to a mean salinity (S_1) of 34.85 $^0/_{00}$. As determined from samples in the upper 150 m., M_2 is the mass of Gulf Stream water corresponding to a mean salinity (S_2) of 36.45 $^0/_{00}$ in the upper 150 m.; S is the resulting salinity of 35.55 $^0/_{00}$, as obtained by computing the mean value of all available T–S curves at the highest points of coinciding properties. The computed proportion of masses was $M_1=1.29\ M_2$, which indicates that a somewhat larger amount of slope water than Gulf Stream was supplied to the mixing process. If all mass separated from the Gulf Stream were to return after mixing, the volume of water returning would be more than double, but such total return seems unlikely.

EFFECT ON ENERGY IN THE GULF STREAM

The departure of part of the dense water to the left side of the Gulf Stream below 300 m. would help to maintain the upper 1,000 m. of the water column at a higher density than would otherwise be the case, and the total mass of dense water would also be increased. In addition, the inflow of dense water at the left side of the Gulf Stream should displace lighter water to the right and consequently increase horizontal pressure gradient across the Stream. Thus, a rotation of mass to the interaction system and back to the Gulf Stream would constitute an energy source contributing to the maintenance, and even intensification, of the Stream. It is hardly possible to assess what proportion of the total complex of individual driving and impeding forces of the Stream such a source of energy would represent; too little is known about that complex. It could be expected, however, that the proportion, although unknown, would be greatest in the late winter and spring, when temperature and density differences between Gulf Stream water and inshore water are large.

SUMMARY

Repeated sections along three transects of the Gulf Stream off Chesapeake Bay in the spring of 1963 revealed a process of interaction between the left flank of the Gulf Stream and the adjacent slope water. The data, though incomplete, suggest the following interpretation of the process:

1. Warm, saline water from the left side of the Gulf Stream was shifted to the left by transient intensified convergence in the slope water–Gulf Stream boundary.
2. This warm water became isolated from the Gulf Stream by divergence near the surface and by upwelling.
3. Intense mixing of the separated Gulf Stream water with the slope water generated a dense water type at depths of about 80 to 180 m.
4. Because of the transient occurrences of unstable mass distribution, a part of the water ($\sigma_t > -27.0$) moved downward and along equal density surfaces and joined with the left side of the Gulf Stream at depths of about 250 to 700 m. Some of the mixed water was probably discharged into secondary streams farther downstream and to the left of the main body of the Gulf Stream.

ACKNOWLEDGMENTS

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INTERACTION OF FOOD LEVEL AND EXPLOITATION IN EXPERIMENTAL FISH POPULATIONS

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ABSTRACT

Nine populations of guppies (*Lebistes reticulatus*) were established in separate aquariums. Food supply was constant for groups of three populations in ratios of 0.5, 1.0, and 1.5 to a "standard" diet. Temperature, light, and space were constant and the same for all populations. After 28 weeks, populations had reached near-asymptotic levels, and mean numbers and weights for each group of three were in the same rank as their food levels.

Twenty-five percent, 33 percent, and 50 percent of the fish were removed per 3-week brood interval for each food-level group of three populations, thus providing nine combinations. Continuation of exploitation at these rates led to relatively stable yields during weeks 59 to 72, after initial declines due to readjustment of populations. Yield curves for each food level revealed relation of yield to exploitation rate and biomass to be independent of amount of food consumed. Maximum yields occurred near the 0.33 (33 percent) exploitation rate for all food levels and represented about 25 percent of the food consumed. Results suggest that if commercially fished populations behave as the experimental ones did, management strategies may be applied independently of amount of food organisms available.

The purposes of laboratory fish-population experiments and their relation to other work in fishery dynamics have been set forth rather fully by Silliman (1948) and Silliman and Gutsell (1958). Briefly, the purposes are to provide experimental measurement of the effect of exploitation on stocks of fish, under as fully controlled environmental conditions as possible. The above authors also pointed out the advantages of the guppy (*Lebistes reticulatus*) as an experimental animal: rapid growth and reproductive rates, small size, and hardiness.

Food supply and exploitation rate must be among the most important factors that determine biomass and yield in exploited fish populations. The response of populations to exploitation is well known, as set forth in such works as Beverton and Holt (1957). The importance of food supply, although not as fully documented, is well recognized. For example, Zheltenkova (1961) adduced data indicating that a decreased supply of food reduced the rate of growth and catches of bream in the Sea of Azov. She also reported a number of qualitative examples in another work (1958) that, although lacking numerical estimates of food amounts, tended to support the thesis that food supply is important in determining yield and rate of growth of several fishes in the U.S.S.R. These examples indicate not only the importance of food level at any given time but also the importance of the great fluctuations in this level that occur from one time to another.

Quantitative support for the idea that fluctuations in food supply would modify fluctuations in fish stocks resulting from other causes was provided early by Jensen (1928). His data on measured amounts of bottom food in certain Danish waters in the fall were significantly correlated with catches of plaice.

Because yield is related to both food supply and rate of exploitation, the interaction of these two is of obvious interest to the fishery manager. Might it be possible, for instance, to harvest a greater percentage of the stock when food supply and abundance are high than when they are low? The experiments described in this report were

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carried out to throw light on this and similar questions, such as precisely how yields are related to exploitation at each food level. Answers were sought by investigating the effects at controlled exploitation and food level on population biomass and yield.

PLAN OF THE EXPERIMENT

Experimental tanks provided for three food levels and three rates of exploitation, a total of nine combinations. Because of limited facilities and personnel, replications were not made. The experience of Silliman and Gutsell (1958) helped to determine the specific food levels and exploitation rates to use. In each test the levels were chosen to bracket the ones that had provided the greatest yield in the previous experiments. Maximum yield for those experiments occurred when the populations were fed a standard diet and when 25 to 50 percent of the fishable stock was removed per 3-week period (the average interval between broods of a female guppy).

For the experiments reported here, food levels of 0.5, 1.0, and 1.5 times the "standard" diet were arbitrarily selected. An arbitrary selection of exploitation rates at 0.25, 0.33, and 0.50 per 3-week period was also made. The resulting nine combinations were assigned by lot to a row of nine experimental tanks, as follows: Tank A, diet 1.0, exploitation rate 0.25; B, 0.5, 0.25; C, 1.5, 0.50; D, 1.0, 0.50; E, 1.5, 0.25; F, 0.5, 0.33; G, 1.0, 0.33; H, 0.5, 0.50; I, 1.5, 0.33.

The plan of the experiment was simple: To start a population of guppies in each tank and allow all to grow until asymptotic size or a close approach to it had been attained. The populations were then exploited at the chosen rates, and this was continued until the yield from each tank became reasonably stable.

MATERIALS AND METHODS

The experiments were conducted from January 30, 1964, through June 17, 1965, at the former Biological Laboratory, Bureau of Commercial Fisheries, Washington, D.C.

FISH TANKS AND EQUIPMENT

Conventional glass-walled aquariums were used as experimental tanks (fig. 1). The water surface in each was 44 by 24 cm.; and the depth, 19 cm. (volume, 20 l.). Each was provided with a cotton-charcoal filter (inside the tank) and an airstone. A pair of small pumps supplied air for both of these fixtures.

The available room illumination was used as a light source. It consisted of two banks of eight 40-watt fluorescent lamps (fig. 1). (Evidence to be presented later in the section "Changes During Exploitation" will support the assumption that differences in amounts of light received by different populations did not confound the interpretation of the experimental results.) All windows were covered, and lights were controlled by a time switch to be on each day from 6 a.m. to 6 p.m.

Refuges for the young fish were provided by fences placed in the left "front" (facing row of tanks with A to I from left to right as in fig. 1) corners of all tanks. Each fence consisted of glass rods supported by plastic rails. The rods were 21 cm. long and were placed vertically to form a fence 15 cm. long. The center of each glass rod (3 mm. in diameter) was 4.5 mm. from the center of the next rod, leaving spaces of 1.5 mm. between rods for the passage of the young fish. Fences were placed in tanks so as to enclose a 45° right triangular space in the corner of each.

A grader for separation of "fry" from "immature" sizes of fish consisted of a plastic box 20 cm. long with ends 10 cm. square. This box was open at the top, and the bottom was composed of plastic rods, 3 mm. in diameter, placed parallel to the longer axis of the box. Because centers of the rods were 5 mm. apart, 2-mm. spaces were left for grading the fish. All fish which would pass through the grader were classified as "fry"; immature fish which would not were classified as "immature."

EXPERIMENTAL DIET AND PROCEDURES

The diet I used was a standard one developed during previous experiments (Silliman and Gutsell, 1958). Food consisted of medium-grade dry tropical fish food, frozen *Daphnia*, and newly hatched *Artemia* nauplii. The dry food was a commercial product containing dried mosquito larvae, dried flies, dried *Daphnia*, fish-liver meal, beef meal, shrimp meal, salmon-egg meal, wheat-germ meal, fish-roe meal, clam meal, fish-bone meal, dried egg yolk, whole wheat meal, dehydrated kelp, dehydrated alfalfa-leaf meal, dehy-

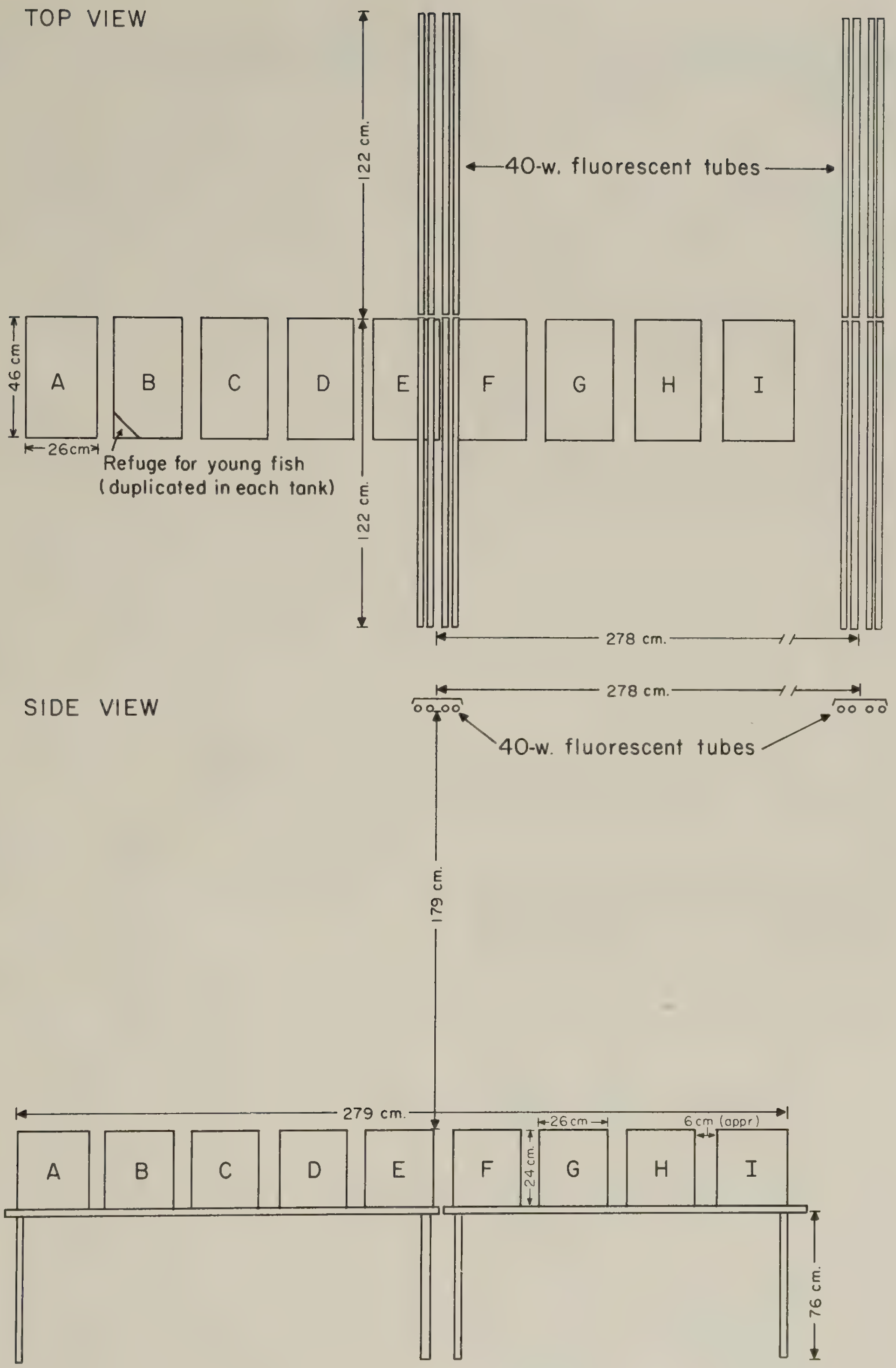
TOP VIEW
122 cm.
40-w. fluorescent tubes
46 cm
26cm
A
B
C
D
E
F
G
H
I
Refuge for young fish
(duplicated in each tank)
122 cm.
278 cm.
SIDE VIEW
278 cm.
40-w. fluorescent tubes
179 cm.
279 cm.
26 cm
6 cm (appr)
24 cm.
A
B
C
D
E
F
G
H
I
76 cm.

FIGURE 1.—General arrangement of tanks and orientation with respect to light fixtures. Door to room was located beyond end of light fixture in upper right corner, and was not visible to fish in tanks.

drated carrot, dehydrated lettuce, dehydrated spinach, and dehydrated water cress.

The following analysis was supplied by the maker:

Crude protein, minimum	40 percent
Crude fat, minimum	3 percent
Crude fibre, maximum	10 percent

Artemia nauplii were produced by placing the dry eggs in 750 ml. of salt water (one level tablespoonful per 750 ml.) and incubating them 2 days at about 24° C. Food was supplied to tanks according to the schedule in table 1. All of the daily food allotment was placed in the tanks at one time. During the early part of the experiment some food fell to the bottom of the tanks uneaten; it was siphoned out before the following day's feeding. When the populations had grown to pre-exploitation sizes, all food was consumed.

TABLE 1.—*Schedule of food supplied to tanks receiving various diets. The "standard" diet is designated 1.0*

Day of week	0.5 diet			1.0 diet			1.5 diet		
	Frozen *Daphnia*	*Artemia* nauplii [1]	Dry food	Frozen *Daphnia*	*Artemia* nauplii [1]	Dry food	Frozen *Daphnia*	*Artemia* nauplii [1]	Dry food
	G.	*G.*	*G.*	*G.*	*G.*	*G.*	*G.*	*G.*	*G.*
Sun	------	------	0.05	------	------	0.10	------	------	0.15
Mon	0.5	0.2	.05	1.0	0.4	.10	1.5	0.6	.15
Tues	.5	.2	.05	1.0	.4	.10	1.5	.6	.15
Weds	.5	.2	.05	1.0	.4	.10	1.5	.6	.15
Thurs	.5	.2	.05	1.0	.4	.10	1.5	.6	.15
Fri	.5	.2	.05	1.0	.4	.10	1.5	.6	.15
Sat	------	.2	.05	------	.4	.10	------	.6	.15
Total	2.5	1.2	.35	5.0	2.4	.70	7.5	3.6	1.05

[1] This represents weight of eggs hatched. Actual weight of nauplii produced, for the "standard" diet was 0.125 mg. (Silliman and Gutsell, 1958). The determination was made by producing duplicate hatches of 0.4 g. of eggs; these hatches were then dried, weighed, and the average weight determined. No data were available to adjust for day-to-day variations in hatching success. The weight of nauplii represented such a small part of the total diet (about 1/100 of 1 percent) that variations would not significantly affect total food available.

The nine populations were started on January 30, 1964. (A list of dates for the numbered weeks of each experiment is given in table 2.) Stocks were from previously established aquariums and consisted of 432 guppies. I segregated the fish into males, females, and "juveniles," the latter including the categories "fry" and "immature" as defined above. All males were placed in a single container and then put into the nine tanks from A to I in succession, one fish at a time. I repeated this process until seven males were in each tank. I used a like process to put eight females in each tank. Similarly, 33 juveniles were placed in each tank, but they were introduced in groups of 10, 10, 10, and 3. Thus, each tank contained 48 fish—7 males, 8 females, and 33 juveniles—chosen in a consistent manner from established aquarium stocks.

Populations were fished (exploited) at 3-week intervals, the approximate time between broods.[1] These rates bracketed the rate previously found to produce maximum yield (Silliman and Gutsell, 1958), which was about 0.33 per 3-week period. The "bracketing" rates were 0.25 and 0.50 per 3-week period. Fishing was done by removing each nth fish for fishing rate $\frac{1}{n}$ and was applied only to the "immature" and "adult" fish, excluding the "fry." "Adults" included all fish whose sex could be determined by external inspection; and "immatures", all others except the "fry" that passed through the grader described above.

Procedures were described in more detail by Silliman and Gutsell (1958), who also reported the technique of weekly counting and weighing the fish. This essentially consisted of counting fish individually and placing them on a strainer. From the strainer fish were transferred to a previously weighed container of water on a balance.

TABLE 2.—*List of calendar weeks included in experiment*

Week No.	Beginning Year, month, and day	Week No.	Beginning Year, month, and day
0	*1964* Jan. 26	37	*1964* Oct. 11
1	Feb. 2	38	18
2	9	39	25
3	16	40	Nov. 1
4	23	41	8
5	Mar. 1	42	15
6	8	43	22
7	15	44	29
8	22	45	Dec. 6
9	29	46	13
10	Apr. 5	47	20
11	12	48	27
12	19		
13	26	49	*1965* Jan. 3
14	May 3	50	10
15	10	51	17
16	17	52	24
17	24	53	31
18	31	54	Feb. 7
19	June 7	55	14
20	14	56	21
21	21	57	28
22	28	58	Mar. 7
23	July 5	59	14
24	12	60	21
25	19	61	28
26	26	62	Apr. 4
27	Aug. 2	63	11
28	9	64	18
29	16	65	25
30	23	66	May 2
31	30	67	9
32	Sept. 6	68	16
33	13	69	23
34	20	70	30
35	27	71	June 6
36	Oct. 4	72	13

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[1] Each brood consists of 6 to 60 young, depending on the size of the female (Innes, 1945).

Total weight of fish, container, and water was determined, and the fish weight obtained by subtraction.

ENVIRONMENTAL CONDITIONS

Although temperature was controlled as closely as possible, there were some variations. These were examined in relation to possible effects on growth or survival. Oxygen determinations were also made, to ascertain if the levels were within those considered adequate for warm-water fishes.

TEMPERATURE

Room air temperature was controlled by a thermostatically regulated window heat pump, which could either heat or cool. Water temperature about 8 cm. below the surface of tanks A, E, and I (fig. 1) was recorded daily at about 8 a.m., noon, and 4 p.m. (Only one reading per day was taken on weekends.) The means indicated reasonably stable temperatures (table 3). No 30-day mean deviated more than 0.7° C. from the grand mean. The means for all three times of day gave some indication that tank A averaged higher than the others, but the greatest excess of A over either E or I was 0.5° C. Likewise, the means for all three tanks indicated that the 4 p.m. reading tended to be lower than the others, but again the greatest departure was 0.5° C. The means of "All 3 by All 3" revealed no consistent trend in temperatures during the experiment. The total range of individual temperature readings during the entire experiment was from 21.1° to 27.2° C.

Table 3.—*Mean temperatures for tanks A, E, and I during three 30-day periods* [1]

Period	Temperature recording time	Mean temperature			
		Tank A	Tank E	Tank I	All 3 tanks
		°C.	*°C.*	*°C.*	*°C.*
Mar. 5–Apr. 21, 1964	8 a.m.	24.4	24.1	24.1	24.2
	Noon	24.5	24.4	24.3	24.4
	4 p.m.	23.9	24.0	24.1	24.0
	All 3 times	24.3	24.2	24.2	24.2
Sept. 16–Nov. 2, 1964	8 a.m.	24.9	24.4	24.6	24.7
	Noon	24.4	24.6	24.5	24.7
	4 p.m.	24.8	24.1	24.3	24.3
	All 3 times	24.8	24.3	24.6	24.6
Apr. 23–June 11, 1965	8 a.m.	24.6	24.3	24.3	24.3
	Noon	24.4	24.1	24.0	24.2
	4 p.m.	23.9	23.8	23.6	23.8
	All 3 times	24.3	24.1	23.9	24.1
All 3 periods	All 3 times	--------	--------	--------	24.3

[1] The period means are based on 30 days in which three daily readings were taken in all three tanks. The period is not based on 30 consecutive days. The days that were excluded from the periods were ones in which fewer than three readings were made (these days usually were on weekends).

The rather small deviations just recorded suggest that temperature was fairly well controlled. Any effects on growth or survival must have been slight, and no further analysis of temperatures seems justified.

OXYGEN CONCENTRATION

Oxygen determinations were made for each tank during March 29 to April 14, 1965. Readings ranged from 4.54 to 5.58 p.p.m., all within or above the 3 to 5 p.p.m. that Lewis (1963) considered adequate for warm-water fishes.

Ozone was used in the tanks to control algae during weeks 56–72. This was supplied by a "Sander Ozonizer" [2] at the rate of 5 mg. per hour. Except for occasional treatments of individual tanks, the 5 mg. per hour was delivered to the main air supply, thus being divided among the nine tanks. Previous tests with fish not included in the experiments produced no mortalities when the entire 5 mg. per hour was supplied to a single 20-l. tank. No relation was noted between growth of algae and food supply or amount of light.

POPULATION CHANGES

For purposes of analysis, the experiment was arbitrarily divided into periods before (weeks 0–28), and after (weeks 29–72) exploitation began. Changes during the first period reflected increases in number and biomass resulting from reproduction and growth. Exploitation was responsible for the major changes in the second period, resulting in initial declines followed by relative stability in both population size and yield.

INITIAL GROWTH OF POPULATIONS

The stocks entered a period of growth in numbers and weight, each stock influenced by the amount of food supplied. Mean numbers and weights each week for the group of three tanks at each food level (tables 4 and 5, and fig. 2) clearly bring out the influence of food supply on growth. Total weights of the stocks were in the same rank as, but not exactly proportional to, amounts of food supplied. During weeks 21 to 28, mean weights for diet levels 0.5, 1.0, and 1.5 were 14.5, 26.0, and 36.6, respectively. These

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[2] Trade names referred to in this publication do not imply endorsement of commercial products.

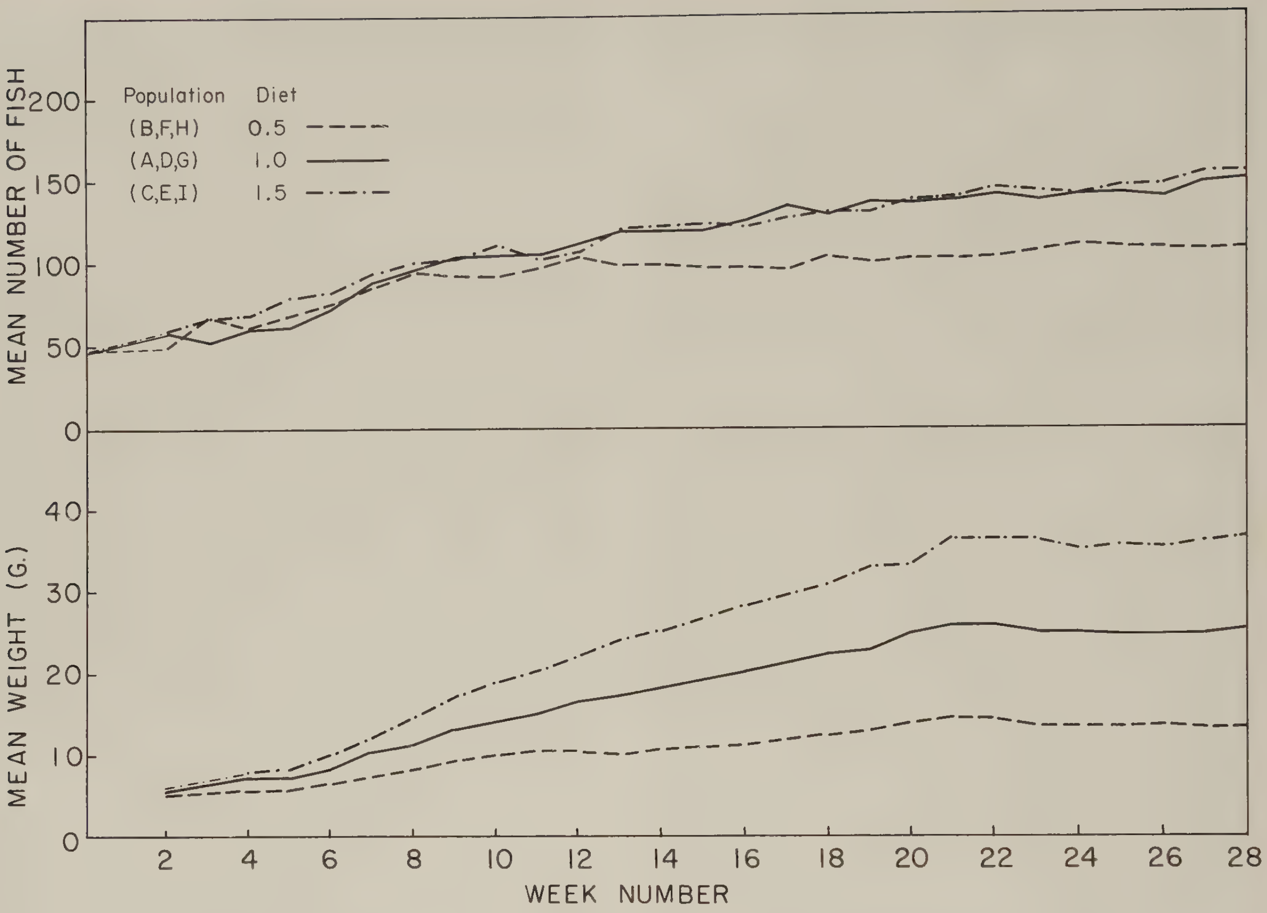

FIGURE 2.—Initial growth of populations. Data are means for the three populations at each diet level.

were in ratios 1.00:1.79:2.52 as compared with the 1:2:3 ratios of the diet levels.

Average numbers of fish fell even farther from the ratios of the diet levels than did the average weights. For weeks 21 to 28 they were 110, 145, and 149 in ratios 1.00:1.32:1.35. Comparison of these ratios with those for average weights indicated that the individual fish averaged larger at the higher diet levels. Weights of individual fish averaged 0.132, 0.179, and 0.246 g., respectively, in populations at diet levels 0.5, 1.0, and 1.5.

These results indicate that the greater biomass at the higher diet levels than at the lowest level was caused by both better survival and more rapid growth of individuals. Growth was the more important factor. The results indicate also somewhat less efficient food use at the higher diet levels than at the lowest, in the sense of the amount of biomass supported by a given amount of food. Thus, the 2.85 g. of food consumed per week (totals for *Daphnia* and dry food from table 1, plus 6 times ½ of 0.000125 g. for *Artemia*), at the 0.5 diet level supported a biomass of 14.5 g., or 5.1 g. per gram of weekly consumption, whereas at the 1.5 diet level the comparable figures are 8.55 g., 36.6 g., and 4.3 g. This loss of efficiency may have been the result of crowding the larger biomass at the higher diet levels into the same amount of space as occupied by the biomass at the lowest diet level. Alternatively, it is possible that such efficiency may simply be a declining function of size in stabilized populations.

TABLE 4.—*Weekly numbers of fish in each lettered tank during period of initial growth, first 28 weeks*

Week No.	0.5 diet				1.0 diet				1.5 diet			
	Tank B	Tank F	Tank H	Tank mean	Tank A	Tank D	Tank G	Tank mean	Tank C	Tank E	Tank I	Tank mean
	No.	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
0	48	48	48	48	48	48	48	48	48	48	48	48
1	(1)	(1)	(1)	--------	(1)	(1)	(1)	--------	(1)	(1)	(1)	--------
2	52	54	45	50	60	47	70	59	86	49	46	60
3	89	51	65	68	43	45	72	53	74	62	66	67
4	58	50	74	61	42	71	70	61	79	59	69	69
5	80	53	78	70	50	71	69	63	100	67	73	80
6	90	61	77	76	66	73	84	74	122	73	73	89
7	122	67	77	87	68	110	89	89	122	75	87	95
8	119	93	75	96	76	121	95	97	121	77	105	101
9	121	83	76	93	113	110	92	105	131	79	99	103
10	121	81	77	93	99	111	107	106	145	95	100	113
11	130	82	82	98	95	125	115	112	136	85	105	109
12	142	92	81	105	97	144	116	119	138	85	103	109
13	120	97	82	100	115	134	114	121	171	94	102	122
14	121	95	83	100	110	140	117	122	166	94	111	124
15	124	94	78	99	103	139	120	121	161	95	120	125
16	122	95	80	99	106	154	119	126	160	93	116	123
17	120	89	83	97	119	155	135	136	167	100	121	129
18	129	102	87	106	113	149	130	131	181	99	117	132
19	122	101	83	102	122	151	141	138	183	97	115	132
20	125	105	85	105	125	151	138	138	203	99	117	140
21	124	103	89	105	121	158	141	140	182	104	138	141
22	126	103	88	106	130	165	134	143	191	127	122	147
23	133	109	88	110	125	163	132	140	198	118	119	145
24	135	114	89	113	129	160	144	144	195	116	119	143
25	132	112	88	111	133	159	141	144	198	122	127	149
26	135	112	87	111	131	152	143	142	193	122	135	150
27	131	111	87	110	133	159	160	151	209	123	139	157
28	127	117	88	111	144	160	155	153	207	122	142	157

[1] Not counted.

TABLE 5.—*Weekly weights of fish in each lettered tank and mean weight per diet during period of initial growth, first 28 weeks*

Week No.	0.5 diet				1.0 diet				1.5 diet			
	Tank B	Tank F	Tank H	Tank mean	Tank A	Tank D	Tank G	Tank mean	Tank C	Tank E	Tank I	Tank mean
	G.	*G.*	*G.*	*G.*	*G.*	*G.*	*G.*	*G.*	*G.*	*G.*	*G.*	*G.*
0	(1)	(1)	(1)	--------	(1)	(1)	(1)	--------	(1)	(1)	(1)	--------
1	(1)	(1)	(1)	--------	(1)	(1)	(1)	--------	(1)	(1)	(1)	--------
2	5.5	4.6	5.9	5.3	6.5	5.5	5.7	5.9	4.8	7.7	6.1	6.2
3	5.3	5.3	6.5	5.7	7.0	6.6	6.5	6.7	6.3	(3)	(3)	--------
4	5.6	5.8	6.5	6.0	8.2	7.1	7.6	7.6	7.8	8.7	7.8	8.1
5	5.3	6.4	6.2	6.0	7.3	7.1	8.8	7.7	9.3	8.3	8.4	8.7
6	6.3	7.6	7.0	7.0	7.8	8.6	10.0	8.8	11.0	10.0	10.3	10.4
7	6.7	8.9	7.7	7.8	9.5	10.5	12.5	10.8	13.5	12.3	12.2	12.7
8	8.3	9.3	8.5	8.7	11.3	11.4	12.0	11.6	16.2	14.5	14.2	15.0
9	8.7	11.0	9.8	9.8	13.0	13.5	13.7	13.4	18.6	17.1	16.4	17.4
10	9.6	10.9	10.4	10.3	13.6	15.0	14.8	14.5	20.0	19.0	18.8	19.3
11	10.0	12.3	10.4	10.9	15.2	16.2	15.8	15.7	21.7	20.5	19.9	20.7
12	10.4	11.2	10.9	10.8	16.6	16.8	17.5	17.0	24.2	22.9	21.0	22.7
13	10.9	10.4	10.9	10.7	17.3	17.6	18.3	17.7	25.8	24.2	22.9	24.3
14	11.4	10.6	11.8	11.3	18.2	18.6	18.9	18.6	26.3	25.8	24.8	25.6
15	12.1	11.4	11.5	11.7	19.4	19.9	19.7	19.7	27.9	27.0	26.6	27.1
16	12.2	11.8	11.8	11.9	20.4	20.4	21.0	20.6	29.7	29.2	27.5	28.8
17	12.6	12.2	12.2	12.3	21.6	21.2	22.3	21.7	31.6	30.2	28.3	30.0
18	13.7	12.8	12.4	13.0	23.0	22.5	23.4	23.0	33.3	31.8	29.2	31.4
19	12.7	13.1	15.2	13.7	22.8	23.2	24.1	23.4	33.8	32.7	33.3	33.3
20	15.6	14.5	14.0	14.7	25.6	24.4	26.4	25.5	35.6	33.6	32.2	33.8
21	17.3	14.2	14.4	15.3	26.0	26.5	27.4	26.6	38.2	39.4	33.3	37.0
22	16.0	14.3	14.9	15.1	26.4	25.8	26.9	26.4	40.5	37.0	33.3	36.9
23	14.6	14.4	13.9	14.3	25.8	24.9	26.3	25.7	40.8	37.6	32.5	37.0
24	14.4	14.2	13.9	14.2	25.5	25.5	26.6	25.9	38.2	35.9	33.0	35.7
25	14.3	14.6	13.7	14.2	25.4	24.4	26.3	25.4	40.0	35.7	32.9	36.2
26	15.2	14.5	14.1	14.6	27.2	(2)	26.6	--------	40.1	35.4	32.5	36.0
27	14.2	14.5	13.7	14.1	25.7	24.9	26.9	25.8	39.5	35.8	34.5	36.6
28	14.1	14.7	13.9	14.2	25.2	25.7	27.8	26.2	38.8	35.6	37.7	37.4

[1] Not weighed.
[2] No record.
[3] Aberrant data discarded.

CHANGES DURING EXPLOITATION

It was desired to have the populations as stable as possible before the start of exploitation. Degree of stability was examined by studying the distribution of the individual populations with respect to the categories "fry," "immature," and "adult." For the 3 weeks immediately before the start of exploitation at each diet level, compositions according to these categories revealed fairly consistent patterns for the 0.5 and 1.0 levels (figs. 3 and 4), both between weeks and between populations. (Weeks of removal were staggered to facilitate the laboratory routine. Thus, exploitation at the 0.5 level began a week after that at the 1.0 level.) The compositions are characteristic of mature populations at or near the asymptotic level—mostly adults that are rather stable in number and much smaller and somewhat more fluctuating numbers of juveniles.

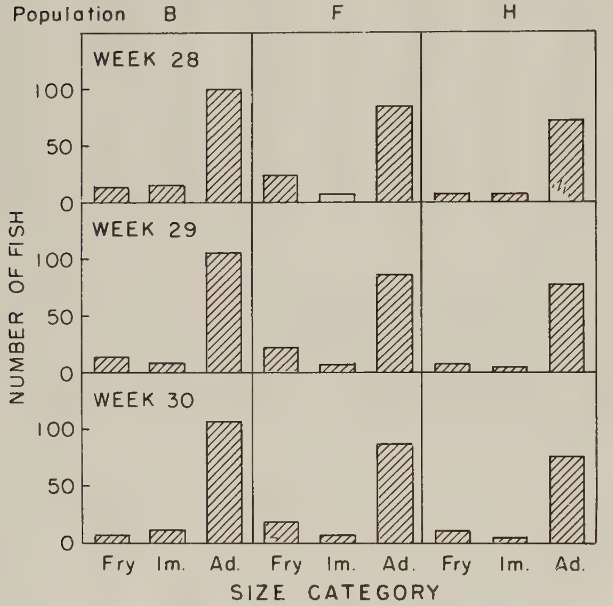

Figure 3.—Composition according to categories "fry," "immature," and "adult" (defined in section "Experimental diet and procedures") of populations at the 0.5 diet level, immediately before exploitation.

Characteristics of the compositions were similar at the 1.5 level (fig. 5) except for the lack of consistency between populations. (Exploitation was delayed 4 weeks in the hope that this inconsistency might disappear.) Here the differences are marked both in total number (as between C and E in week 34) and in percentage composition (as between C and I in week 32). These differences are surprising among populations held for more than 30 weeks under conditions of food supply, temperature, light, and space as nearly identical as possible. No ready explanation could be found among other conditions of the environment or among procedures of handling the fish. Probably genetic differences were not averaged out among the rather small numbers of adults (15) in the initial populations, in spite of the method of selection (section, "Initial growth of populations"). The differences may also have resulted from variations in gravidity among the eight adult females in each initial population. Support for some explanation related to the initial populations is found in the fact that C exceeded E and I in number and weight almost from the start of the experiment (weeks 2 to 28, table 3; weeks 5 to 20 and 22 to 28, table 4).

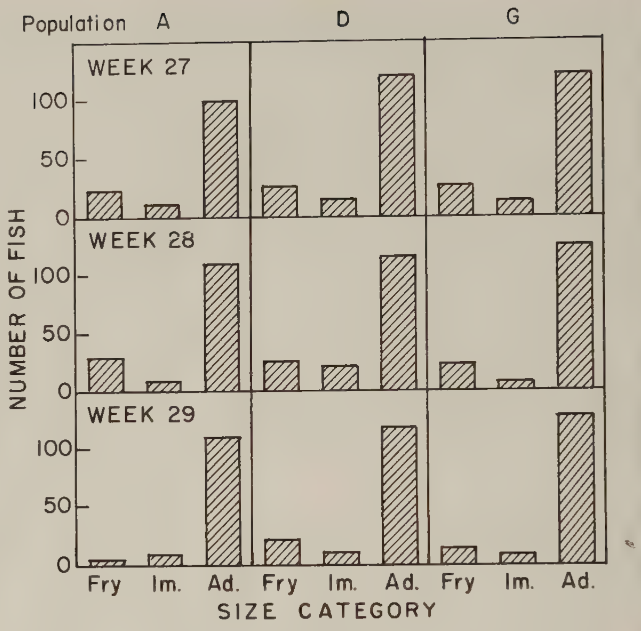

Figure 4.—Composition according to categories "fry," "immature," and "adult" (defined in section "Experimental diet and procedures") of populations at the 1.0 diet level, immediately before exploitation.

The differences among populations at the 1.5 diet level persisted, even though the start of exploitation was delayed 4 weeks beyond that for

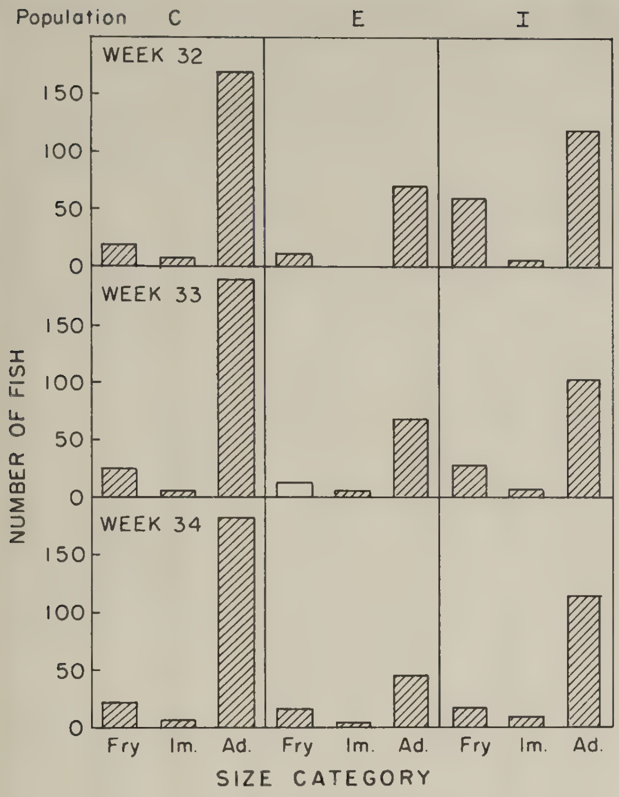

FIGURE 5.—Composition according to categories "fry," "immature," and "adult" (defined in section "Experimental diet and procedures") of populations at the 1.5 diet level, immediately before exploitation.

the other six populations. I decided to proceed with exploitation of the 1.5 level group because of the substantial amount of time and effort already invested and the desire to have yields comparable with those for the other populations. This decision was supported by the fact that compositions were fairly stable within populations (fig. 5) even though discrepant between them.

Response of the populations to exploitation is indicated by the mean numbers and weights for each diet level (tables 6 to 9 and fig. 6). The saw-tooth pattern of reduction by removals and subsequent recovery is characteristic. As pointed out by Silliman and Gutsell (1958), this kind of variation reflects the resilience of natural populations as long as exploitation rates are not high enough to cause extinction.

As was also mentioned by Silliman and Gutsell, population weights are more stable than population numbers, since the latter are affected more by entrance and mortality of broods of fry. The weights reveal the typical decline in population size after the inception of exploitation, followed by near stability during the final weeks of the experiment. Although populations at all three diet levels decreased in biomass under exploitation, they maintained the preexploitation rank, which was the same as that of the diet levels.

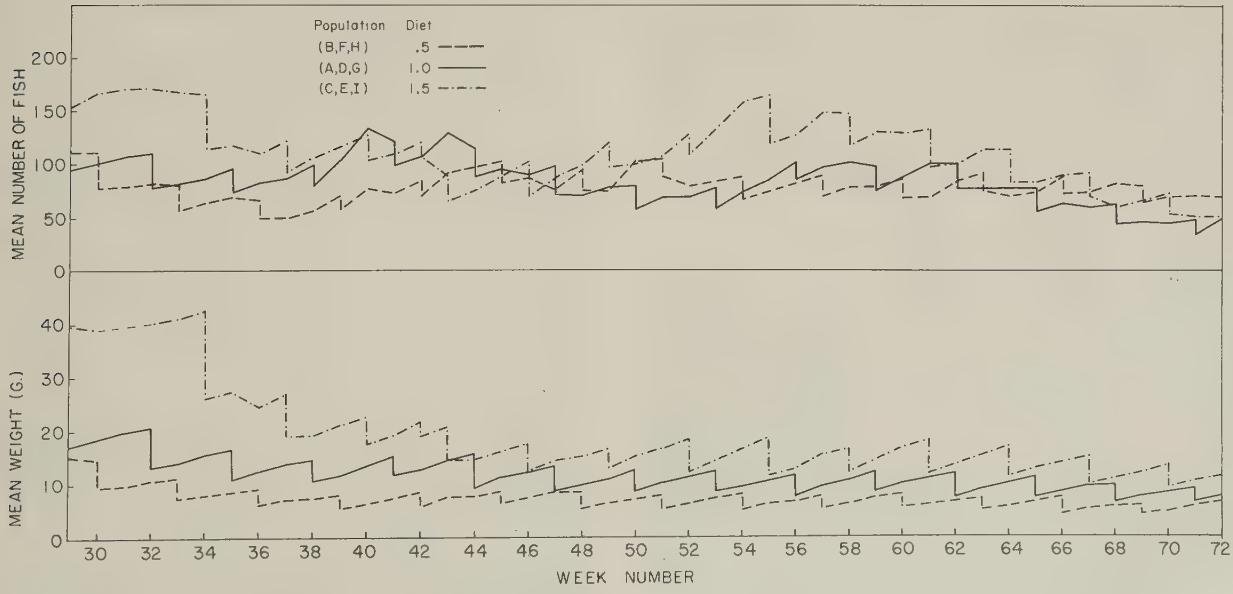

FIGURE 6.—Response of populations to exploitation. Data are means for each diet level.

TABLE 6.—*Weekly numbers and food-level means for each tank during period of exploitation; postremoval numbers for removal weeks were obtained by subtracting numbers removed (table 7); exploitation rates are indicated in parentheses. Exploitation was started week 29 for 1.0 diet, week 30 for 0.5 diet, and week 34 for 1.5 diet*

Week No.	0.5 diet				1.0 diet				1.5 diet			
	Tank B (0.25)	Tank F (0.33)	Tank H (0.50)	Tank mean	Tank A (0.25)	Tank D (0.50)	Tank G (0.33)	Tank mean	Tank C (0.50)	Tank E (0.25)	Tank I (0.33)	Tank mean
	No.	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
29	127	118	91	112	122	158	148	143	204	126	133	154
30	127	114	93	111	104	90	110	101	217	141	141	166
31	101	80	52	78	105	104	110	106	217	143	150	170
32	97	83	67	82	119	93	119	110	200	126	184	170
33	100	87	54	80	96	52	91	80	221	142	138	167
34	90	65	34	63	99	62	93	85	211	158	141	170
35	98	72	36	69	95	71	123	96	131	109	111	117
36	82	69	46	66	73	79	95	82	133	69	124	109
37	70	50	27	49	75	77	106	86	146	74	142	121
38	73	62	34	56	90	74	133	99	107	94	118	106
39	93	72	45	70	107	71	134	104	129	109	111	116
40	82	62	83	76	92	134	172	133	135	122	121	126
41	85	59	72	72	98	131	131	120	114	112	100	109
42	92	97	60	83	82	94	143	106	136	118	106	120
43	106	97	70	91	115	113	157	128	89	97	77	88
44	114	99	71	95	94	101	149	115	68	65	91	75
45	126	110	66	101	80	104	100	95	70	83	112	88
46	107	91	60	86	82	101	85	89	73	92	139	101
47	110	63	51	75	91	108	91	97	77	45	137	86
48	106	122	53	94	69	76	61	69	73	60	160	98
49	87	100	38	75	67	88	75	77	75	112	174	120
50	88	131	85	101	71	89	76	79	39	105	154	99
51	94	135	84	104	101	53	52	69	29	98	193	107
52	71	104	63	79	88	51	67	69	57	130	198	128
53	70	109	69	83	101	50	81	77	76	145	175	132
54	70	125	65	87	109	26	87	74	86	172	220	159
55	63	118	42	74	116	39	101	85	88	159	247	165
56	70	117	55	81	150	52	102	101	106	58	216	127
57	80	121	65	89	148	49	95	97	128	81	234	148
58	74	116	43	78	141	55	107	101	119	78	242	146
59	75	111	47	78	141	56	98	98	108	87	192	129
60	109	105	46	87	139	44	81	88	107	80	196	128
61	90	88	25	68	135	44	122	100	110	95	194	133
62	86	104	62	84	150	49	94	98	63	85	152	100
63	115	107	51	91	120	33	77	77	66	129	148	114
64	97	81	33	70	120	36	74	77	68	126	149	114
65	103	86	33	74	109	31	89	76	39	105	103	82
66	108	88	69	88	88	20	78	62	54	110	102	89
67	97	76	49	74	93	26	60	60	59	112	106	92
68	121	76	49	82	92	28	65	62	32	82	67	60
69	118	74	47	80	68	19	50	46	33	81	85	66
70	118	64	28	70	68	18	47	44	33	94	93	73
71	107	78	29	71	79	21	44	48	20	65	68	51
72	102	74	31	69	77	11	58	49	26	63	66	52

YIELDS

Removals during the period of exploitation were comparable to the catches of commercial fisheries and provided information on stabilized yields. Data were analyzed both to determine when relative stability began and to measure the relation of yield to amount of food consumed.

COMPARATIVE YIELDS

Yields as well as population sizes were more stable in weights than in numbers; therefore, yields were studied in terms of weight. The course of yield for each population during the exploitation period (table 9 and fig. 7) included an initial period of decline as the populations adjusted themselves to removals. This decrease was followed by a period of relative stability beginning about week 49.

Even within the relatively stable period, yields showed considerable irregularity. This phenomenon resulted from variations in the response of the populations to exploitation and from deviations of the percentages removed from the exact nominal exploitation rates. The latter deviations occurred because the removal rates were applied on the basis of numbers of fish rather than weights. Some of this random variability is averaged out in means of yields for three 14- or 15-week subperiods covering the entire period of exploitation (table 9 and fig. 8). These means again reflect the initial period of decline, followed by more stable yields.

The final period, including weeks 59 to 72, was one of fairly stable yield (fig. 7). Mean yields for this period (fig. 8) ranked the same according to exploitation rate for the 1.0 and 1.5 diets. Yields at the 0.5 diet were nearly identical. The period including weeks 59 to 72 fairly well fulfilled the planned objective of "a reasonably stable yield" (section, "Plan of the Experiment"), and data from it were used in the study of relation between food level and exploitation rates. Results from this period had the additional advantage of being

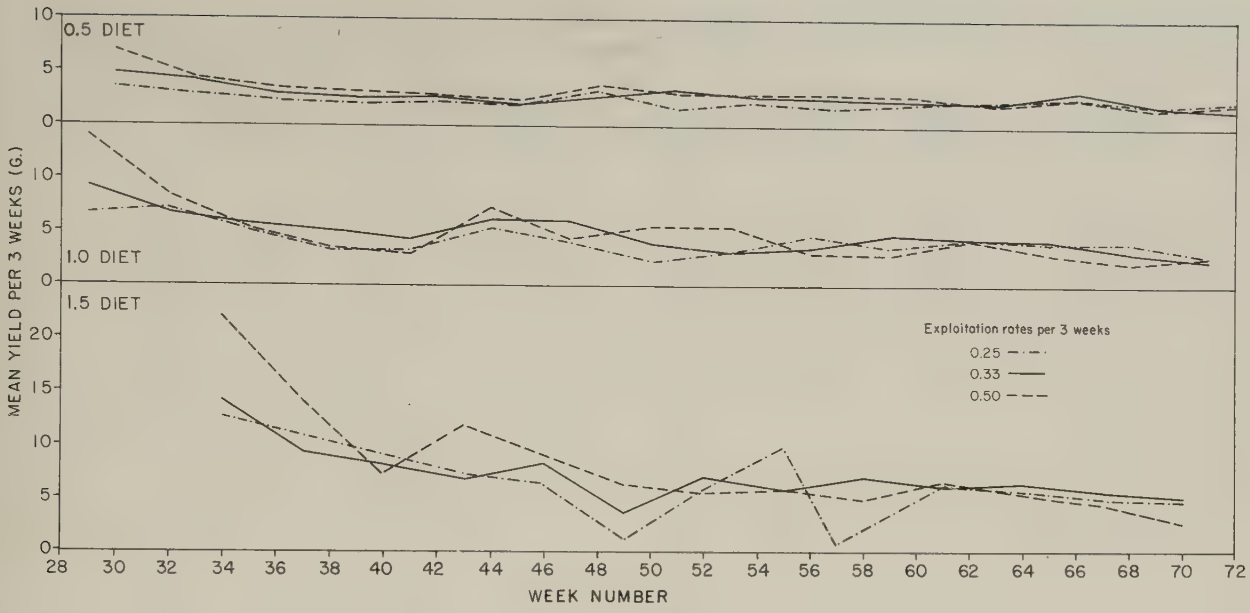

Figure 7.—Yield per three weeks of each population during period of exploitation.

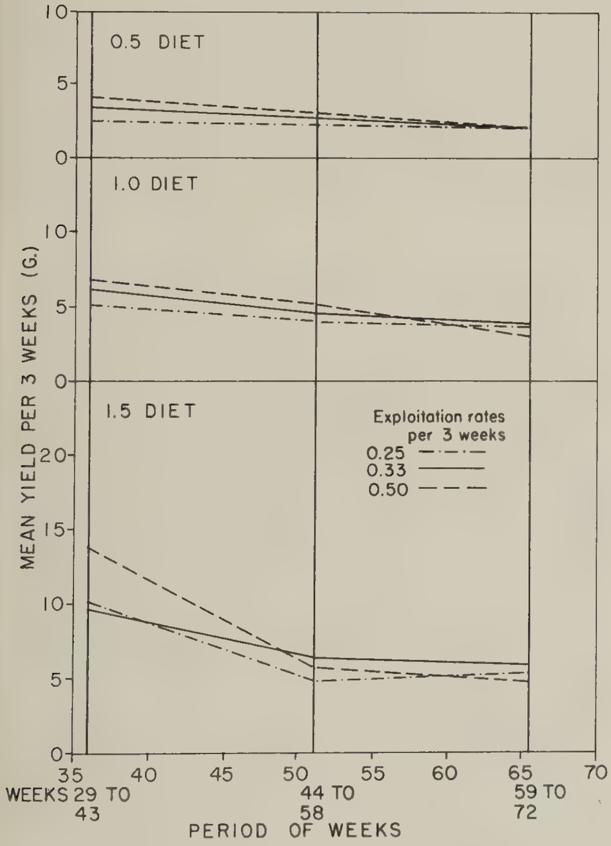

Figure 8.—Mean yields for three 14- or 15-week periods. Location of vertical lines along horizontal scale indicates center of each period.

free from the irregularities in removals and mortalities that occurred at the 1.5 diet level during weeks 37 to 57 (table 7, footnotes).

RELATION BETWEEN YIELD AND FOOD LEVEL

Data in the preceding section showed that yields at the 1.0 and 1.5 diets were related to exploitation rate, but that no such relation was detectable at the 0.5 diet. The available data may now be brought together in an attempt to answer such questions as that posed in the introduction: "Might it be possible, for instance, to harvest a greater percentage of the stock when food supply and abundance are high than when they are low?" It is instructive here to relate the yields to the average total weight or biomass of the populations (table 10). Because the populations were allowed to reach asymptotic size or a close approach to it, an additional point for each yield-biomass curve is available—that at zero rate of exploitation. If small deviations are charged to random variability, the appropriate curves (fig. 9) reveal a regular relation among exploitation rate, biomass, and yield at each diet level (curves fitted by inspection).

The curves suggested that the relation of yield to exploitation rate tends to be independent of diet level. Absolute yields were obviously dependent on amount of food available, but the greatest yield at each diet level occurred at or

TABLE 7.—*Numbers removed (yields) for each diet and exploitation rate; exploitation rates are indicated in parentheses*

Week No.	0.5 diet				1.0 diet				1.5 diet			
	Tank B (0.25)	Tank F (0.33)	Tank H (0.50)	Tank mean	Tank A (0.25)	Tank G (0.33)	Tank D (0.50)	Tank mean	Tank E (0.25)	Tank I (0.33)	Tank C (0.50)	Tank mean
	No.	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
29					29	45	68	47				
30	29	31	41	33								
31												
32					23	35	40	33				
33	24	25	23	24								
34									29	43	95	56
35					19	25	24	23				
36	18	16	15	16								
37									[1] 0	30	55	28
38					16	23	24	21				
39	14	14	12	13								
40									[1] 0	30	41	24
41					14	24	27	22				
42	12	13	18	14					0	0	[2] 43	14
43									22	24	24	23
44					18	33	32	28				
45	18	16	26	20								
46									[3] 71	24	[4] 0	32
47					18	28	35	27				
48	15	21	21	19								
49									11	27	36	25
50					15	21	30	22				
51	17	21	15	18								
52									15	35	13	21
53					14	16	24	18				
54	17	20	23	20								
55									[3] 72	43	24	46
56					18	19	12	16				
57	13	24	23	20					[5] 15			
58										46	27	29
59					22	24	23	23				
60	14	23	21	19								
61									19	47	46	37
62					24	24	18	22				
63	14	22	11	16								
64									15	45	33	31
65					24	24	15	21				
66	14	19	17	17								
67									20	31	18	23
68					24	20	7	17				
69	14	18	15	16								
70									20	23	16	20
71					17	13	9	13				
72	15	14	16	15								

[1] Removals omitted because of accidental mortalities in week 36.
[2] Removals by error; added to week 43 removals in subsequent treatment.
[3] Includes accidental mortality.
[4] Omitted because of erroneous removals in week 43.
[5] Accidental mortality considered to replace removals due in week 58.

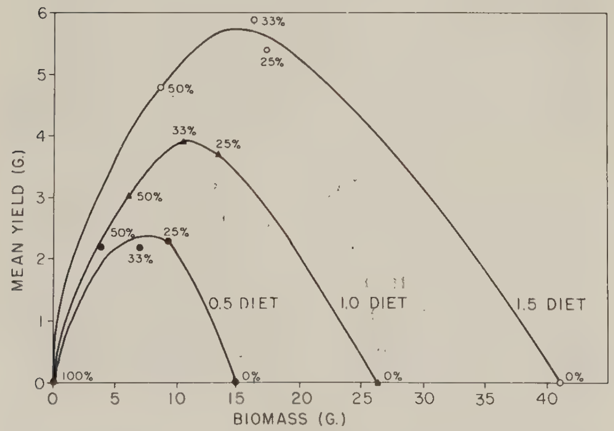

FIGURE 9.—Curves indicating relation of yield per 3-week brood interval to biomass and exploitation rate (indicated percentages) at each diet level. Points indicated for 0 percent exploitation rate are average population levels for the 3 weeks immediately before exploitation.

near the 0.33 exploitation rate (assuming that the different exploitation-yield relation at the 0.5 diet was due to random variation rather than a real difference in the relation). If the apparent independence of the exploitation-yield relation from food level reflects what happens in commercially fished populations, the finding is significant to fishery administration. Such independence would mean that the same management strategy might be applied when food organisms are scarce as when they are abundant.

From the viewpoint of the commercial fisherman, an exploited population is a machine for converting aquatic food to marketable fish flesh. It is of interest to see how efficiently our model of the machine operated at each food level. Maxima of the yield curves (fig. 9) indicate yields per 3 weeks of about 2.4, 3.9, and 5.8 g. at the 0.5, 1.0,

TABLE 8.—*Weekly weights and food-level means for each tank during period of exploitation; postremoval weights for removal weeks were obtained by subtracting weights removed (table 9); exploitation rates are indicated in parentheses. Exploitation was started week 29 for 1.0 diet, week 30 for 0.5 diet and week 34 for 1.5 diet*

Week No.	0.5 diet				1.0 diet				1.5 diet			
	Tank B (0.25)	Tank F (0.33)	Tank H (0.50)	Tank mean	Tank A (0.25)	Tank D (0.50)	Tank G (0.33)	Tank mean	Tank C (0.50)	Tank E (0.25)	Tank I (0.33)	Tank mean
	G.	*G.*	*G.*	*G.*	*G.*	*G.*	*G.*	*G.*	*G.*	*G.*	*G.*	*G.*
29	14.2	15.3	17.5	15.7	26.1	26.8	28.4	27.1	45.2	37.5	35.9	39.5
30	14.6	15.5	14.7	14.9	19.9	14.9	20.2	18.3	42.2	38.1	37.4	39.2
31	11.5	10.1	8.2	9.9	21.0	16.9	21.5	19.8	[1]	41.0	37.6	--------
32	11.9	11.3	8.9	10.7	22.0	17.4	22.6	20.7	42.2	39.5	39.0	40.2
33	12.1	12.0	9.4	11.2	15.6	10.1	16.6	14.1	43.7	40.8	38.6	41.0
34	9.6	8.3	5.9	7.9	17.2	11.7	18.0	15.6	45.7	42.7	39.1	42.5
35	10.3	9.0	6.8	8.7	17.6	13.2	19.2	16.7	23.6	30.8	27.7	27.4
36	10.9	9.4	7.3	9.2	14.0	9.0	14.8	12.6	25.8	19.8	28.4	24.7
37	8.7	8.1	4.9	7.2	15.3	10.1	16.0	13.8	30.0	20.5	30.6	27.0
38	9.4	7.9	5.1	7.5	15.8	11.3	17.0	14.7	14.3	21.5	21.9	19.2
39	9.7	8.5	6.1	8.1	12.8	9.2	13.2	11.7	16.3	23.4	23.4	21.0
40	7.8	7.0	4.5	6.4	14.2	11.0	14.7	13.3	17.2	25.4	25.4	22.7
41	8.7	7.8	5.5	7.3	16.0	12.6	16.7	15.1	12.6	26.0	19.0	19.2
42	10.2	8.6	6.8	8.5	13.8	10.5	14.5	12.9	15.7	28.3	21.3	21.8
43	8.6	7.1	7.2	7.6	15.3	12.5	15.2	14.3	9.5	30.4	22.4	20.8
44	8.6	8.2	6.5	7.8	16.5	13.8	16.8	15.7	7.5	17.1	18.7	14.4
45	10.1	9.3	7.2	8.9	12.9	8.6	12.2	11.2	9.6	18.5	20.2	16.1
46	9.1	8.2	6.1	7.8	13.6	9.6	13.7	12.3	12.2	19.8	21.3	17.8
47	9.8	9.3	6.6	8.6	15.0	11.6	14.3	13.6	14.2	14.1	15.0	14.4
48	10.1	9.1	7.1	8.8	11.6	8.3	9.8	9.9	14.6	14.6	16.1	15.1
49	7.6	7.3	4.2	6.4	12.5	9.0	11.2	10.9	16.2	15.7	18.2	16.7
50	8.5	8.1	5.3	7.3	14.0	10.7	13.0	12.6	12.2	16.9	16.6	15.2
51	9.3	9.3	5.6	8.1	13.3	6.8	10.3	10.1	11.3	19.0	19.5	16.6
52	8.4	6.9	3.7	6.3	14.0	8.0	11.5	11.2	12.5	21.3	21.5	18.4
53	9.0	7.9	4.6	7.2	15.8	9.2	12.8	12.6	8.5	17.7	17.1	14.4
54	9.7	8.8	5.7	8.1	12.2	4.8	11.1	9.4	10.2	19.6	19.6	16.5
55	7.9	6.9	4.3	6.4	13.2	5.9	12.9	10.7	12.3	22.3	21.6	18.7
56	8.5	7.5	4.4	6.8	15.2	6.6	13.6	11.8	7.5	13.5	17.3	12.8
57	9.4	8.4	5.9	7.9	12.2	5.0	11.3	9.5	9.6	16.0	20.6	15.4
58	8.6	6.9	3.6	6.4	13.1	6.4	12.0	10.5	11.3	16.1	22.0	16.5
59	10.3	7.9	4.7	7.6	14.9	7.7	14.3	12.3	8.4	18.0	16.6	14.3
60	10.8	8.1	5.6	8.2	13.1	6.5	10.6	10.1	10.9	20.0	18.9	16.6
61	9.2	6.5	3.6	6.4	14.7	7.6	11.7	11.3	12.6	21.6	20.7	18.3
62	9.5	7.2	4.4	7.0	15.8	8.5	12.1	12.1	8.2	17.5	16.3	14.0
63	10.3	7.9	4.3	7.5	12.1	5.5	9.6	9.1	10.6	18.3	16.6	15.2
64	8.8	6.4	2.9	6.0	13.5	6.7	10.7	10.3	12.3	19.5	20.1	17.3
65	9.6	7.5	3.8	7.0	14.5	8.2	11.2	11.3	8.6	15.6	14.7	13.0
66	10.3	8.0	4.5	7.6	11.6	5.7	8.6	8.6	8.4	17.3	16.5	14.1
67	8.2	6.0	2.6	5.6	13.0	6.4	10.0	9.8	9.5	18.2	18.0	15.2
68	8.8	6.2	3.2	6.1	13.7	6.0	10.9	10.2	5.6	14.8	13.5	11.3
69	8.8	7.0	3.8	6.5	11.6	4.3	8.2	8.0	6.6	16.0	14.6	12.4
70	7.8	5.5	2.5	5.3	12.5	4.9	8.8	8.7	8.0	18.3	15.7	14.0
71	8.2	6.6	4.0	6.3	13.1	5.3	10.4	9.6	5.9	14.6	12.6	11.0
72	9.7	6.9	4.6	7.1	11.6	3.1	9.2	8.0	6.4	15.7	13.6	11.9

[1] Aberrant datum discarded.

and 1.5 diet levels, respectively. Amounts of food consumed at these levels were 8.55, 17.10, and 25.65 g. per 3 weeks (sum of weekly totals for *Daphnia* and dry food plus 6 [0.000125 × diet ratio] for *Artemia*, all multiplied by 3, table 1); thus, conversion efficiencies were 0.28, 0.23, and 0.23. Again, the small difference at the 0.5 diet level probably is not significant. For practical purposes the conversions at all three diet levels are identical and are close to the 0.20 reported by Silliman and Gutsell (1958).

I conclude that efficiency of food conversion, as well as relation between exploitation rate and yield, is independent of amount of food available for the laboratory populations within the range of observation. Management strategies for commercially fished populations that behave in this manner can be applied with the expectation of the same conversion efficiency regardless of the abundance of available food organisms.

This finding seems to be contrary to that reported under "Initial Growth of Populations." It is noteworthy, however, that the lesser efficiency at the two higher diet levels, mentioned there, occurred when the populations were stabilized at near asymptotic levels. Composition of such stabilized populations is different from that of exploited populations, and the growth reactions could well be different also.

The relation of food conversion efficiency to average size of individual fish can be examined by comparing the average weights with the food conversions for each of the nine populations during the exploitation period (weeks 59–72, data from tables 10 and 6, plus food amounts quoted above). L. M. Dickie (personal communication) has pointed out to me that if conversion efficiency be plotted as a regression on average body weight, there is a significant negative correlation (line is $E=0.317-0.667W$, where E is conversion efficiency as above, W is average body weight, and $r=-0.90$ and $P<0.01$). This determination sup-

TABLE 9.—*Weights removed (yields) for each diet and exploitation rate; exploitation rates are indicated in parentheses*

Week No.	0.5 diet				1.0 diet				1.5 diet			
	Tank B (0.25)	Tank F (0.33)	Tank H (0.50)	Tank mean	Tank A (0.25)	Tank G (0.33)	Tank D (0.50)	Tank mean	Tank E (0.25)	Tank I (0.33)	Tank C (0.50)	Tank mean
	G.	*G.*	*G.*	*G.*	*G.*	*G.*	*G.*	*G.*	*G.*	*G.*	*G.*	*G.*
29					6.7	9.3	14.1	10.0				
30	3.6	4.9	7.0	5.2								
31												
32					7.3	6.9	8.5	7.6				
33	2.9	4.2	4.5	3.9								
34									12.8	14.2	22.2	16.4
35					5.2	5.8	5.5	5.5				
36	2.3	2.9	3.6	2.9								
37									[1].0	9.5	14.2	7.9
38					3.4	5.2	3.6	4.1				
39	2.1	2.6	3.2	2.6								
40									[1].0	8.3	7.3	5.2
41					3.2	4.4	3.0	3.5				
42	2.3	2.7	2.9	2.6								
43									7.4	6.8	[2]8.4 3.5	8.7
44					5.5	6.2	7.4	6.4				
45	1.9	2.0	2.4	2.1								
46									[3]6.5	8.4	[4].0	5.0
47					4.1	6.1	4.5	4.9				
48	3.4	2.8	3.8	3.3								
49									1.3	3.7	6.4	3.8
50					2.3	4.0	5.6	4.0				
51	1.6	3.4	3.1	2.7								
52									6.0	7.1	5.6	6.2
53					3.3	3.2	5.6	4.0				
54	2.4	2.7	3.0	2.7								
55									[3]10.0	5.9	6.0	7.3
56					4.9	3.6	3.1	3.9				
57	1.7	2.6	3.0	2.4								
58									[5].8	7.1	5.0	4.3
59					3.6	4.8	2.9	3.8				
60	2.2	2.1	2.8	2.4								
61									6.2	6.1	6.6	6.3
62					4.4	4.4	4.3	4.4				
63	2.3	2.2	1.9	2.1								
64									5.8	6.5	5.5	5.9
65					4.0	4.2	3.0	3.7				
66	2.7	3.3	2.7	2.9								
67									5.0	5.7	4.5	5.1
68					4.1	3.6	2.1	3.3				
69	1.8	2.0	1.6	1.8								
70									4.8	5.2	2.7	4.2
71					2.6	2.4	2.7	2.6				
72	2.4	1.5	2.2	2.0								
Mean												
29–43	2.6	3.5	4.2		5.2	6.3	6.9		10.1	9.7	13.9	
44–58	2.2	2.7	3.1		4.0	4.6	5.2		4.9	6.4	5.8	
59–72	2.3	2.2	2.2		3.7	3.9	3.0		5.4	5.9	4.8	

[1-5] Footnotes on Table 7.

TABLE 10.—*Average biomass and yield per tank per 3 weeks for preexploitation asymptotic levels, and for levels during weeks 59 to 72. Exploitation rates are fractions removed per 3-week brood interval*

Exploitation rate	0.5 diet		1.0 diet		1.5 diet	
	Biomass	Yield	Biomass	Yield	Biomass	Yield
	G.	*G.*	*G.*	*G.*	*G.*	*G.*
0.00	[1] 14.9	0.0	[1] 26.4	0.0	[1] 41.2	0.0
0.25	[2] 9.3	[3] 2.3	[2] 13.3	[3] 3.7	[2] 17.5	[3] 5.4
0.33	[2] 7.0	[3] 2.2	[2] 10.5	[3] 3.9	[2] 16.3	[3] 5.9
0.50	[2] 3.9	[3] 2.2	[2] 6.2	[3] 3.0	[2] 8.7	[3] 4.8

[1] Taken as average of the weights for the three populations during the 3 weeks immediately preceding exploitation. Weeks were as follows: 0.5 diet, 28–30; 1.0 diet, 27–29; 1.5 diet, 32–34. Data from tables 5 and 8.
[2] Data from table 8.
[3] Data from table 9.

ports the contention (Paloheimo and Dickie, 1965) that . . . "within a life-history stanza a given food abundance leads to a higher production of replaceable fish flesh if the producing population consists of the smaller more efficient fish than if it consists of the larger fish." He further pointed out that this regression line might be the population counterpart of the "K-curve" which Paloheimo and Dickie developed for individual fish

$$(K_1=\frac{\Delta W}{R\Delta t}=e^{-a-bR},$$

where W is body weight, R is rations, and a and b are empirical constants).

The fact that the "K-curve" is an exponential relation, whereas the guppy relation is linear, may stem from the wide range of sizes of individual fish in the guppy populations (about 10–40 mm. in length). It may also result from the chief method of population control among guppies—cannibalism. This behavior causes the food of the larger fish to pass through two or more trophic levels, with a consequent lowering of conversion efficiency. Obviously, such an effect would be the more pronounced the larger the average size of individual fish in the population, as long as smaller fish are present for prey, as was true for all populations during the exploitation period.

SUMMARY

1. Nine experimental populations of the guppy, *Lebistes reticulatus*, were established in 20-l. aquariums.

2. Groups of three populations selected by lot were fed at rates 0.5, 1.0, and 1.5 times the "standard" diet.

3. Amount of food, temperature, space, and light were held constant during the course of the experiment.

4. During weeks 21 to 28 of the experiment, mean weights of populations at the 0.5, 1.0, and 1.5 diet levels were 14.5, 26.0, and 36.6 g., respectively; mean numbers of fish were 110, 145, and 149.

5. The greater mass of the populations at the higher diet levels than at the lowest reflected faster growth more than better survival.

6. Exploitation of the populations in each diet level group of three was applied at rates of 0.25, 0.33, and 0.50 per 3-week reproductive period. There were, thus, nine diet-exploitation combinations. Exploitation was started during weeks 29 to 34, when the composition of the populations was reasonably stable, and continued to the end of the experiment during weeks 70 to 72.

7. Populations responded to exploitation with an initial drop in numbers and weight, followed by near stability in weight at new lower levels (numbers were less stable, owing to entrance and mortality [through cannibalism or otherwise] of broods of new-born fish).

8. Yields in weight during the final 14 weeks of the experiment were reasonably stable and were used in the study of the interaction between food level and exploitation.

9. Curves of yield as related to biomass and exploitation rate at each diet level showed that the relation of yield to exploitation rate was independent of diet level.

10. Yields were maximum near the 0.33 exploitation rate for all diet levels, and absolute amounts were 2.4, 3.9, and 5.8 g. per 3-week period for the 0.5, 1.0, and 1.5 diets, respectively.

11. The maximum yields represented conversion of about 25 percent of the food consumed, for all three diet levels.

12. Results suggest that, to the extent that commercially fished populations behave similarly to the laboratory populations, management strategies may be applied regardless of abundance of food organisms.

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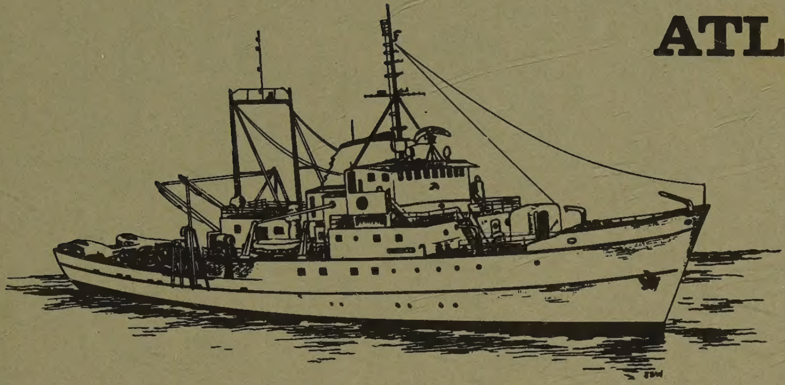

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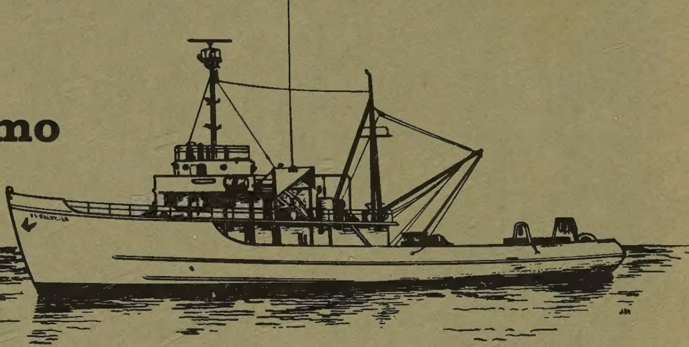

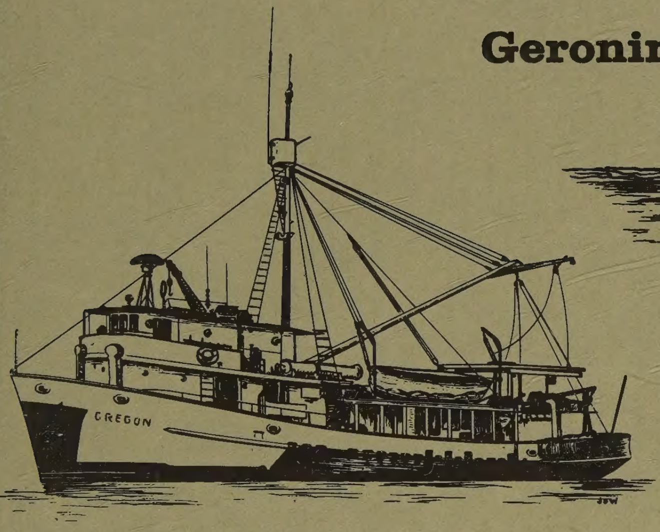

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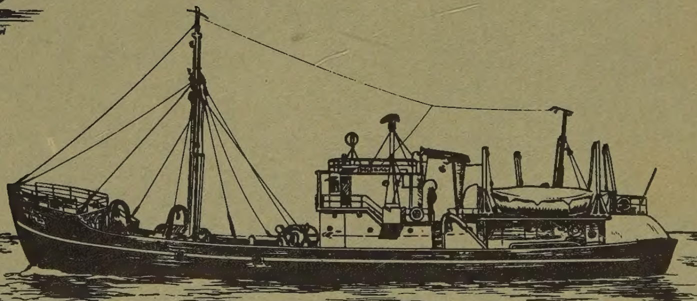

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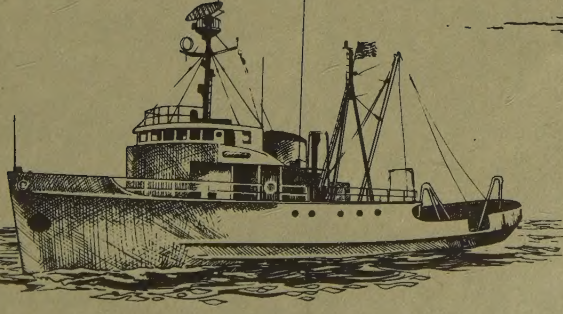

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